MÉMOIRES
DU MUSÉUM
NATIONAL
D'HISTOIRE
NATURELLE

TOME 162

ZOOLOGIE

1994

# *Actes de la 4ème Conférence internationale des Polychètes*

Coordonné par

*Jean-Claude* DAUVIN
*Lucien* LAUBIER
*Donald* REISH

4TH INTERNATIONAL POLYCHAETE CONFERENCE

ANGERS FRANCE 1992

Source : MNHN, Paris

# MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

Directeur de la publication (*Editor-in-chief*) : Jean-Lou JUSTINE
Rédacteurs (*Editors*) : Jean-Marie BETSCH, Philippe BOUCHET, Christian ERARD & Jean-Lou JUSTINE
Secrétariat (*Secretary*) : Bernadette CHARLES
Adresse (*Address*)
Mémoires du Muséum national d'Histoire naturelle
57, rue Cuvier
75005 Paris (France)
Tél. [33] (1) 40 79 34 37

Les *Mémoires du Muséum national d'Histoire naturelle* publient des travaux originaux majeurs, tels que des monographies ou des volumes à auteurs multiples. Les auteurs sont invités, pour toutes les questions éditoriales, à prendre contact avec le directeur de la publication. Les manuscrits peuvent être en français ou en anglais.

*The* Mémoires du Muséum national d'Histoire naturelle *publishes major original contributions, such as monographs or multi-authored volumes. Prospective authors should contact the Editor-in-chief. Manuscripts in French or English will be considered.*

SERVICE DE VENTE
DES ÉDITIONS DU MUSÉUM
57, rue Cuvier
75005 Paris
Tél. : [33] (1) 40 79 37 00
Fax : [33] (1) 40 79 38 40
Telex MUSNAHN 202641 F

*UNIVERSAL BOOK SERVICES*
*Dr. W. BACKHUYS*
*P.O. Box 321*
*2300 A.H. Leiden*
*The Netherlands*
*Tel. : [31] (71) 17 02 08*
*Fax : [31] (71) 17 18 56*

Parution et prix irréguliers. Les ordres permanents d'achat et les commandes de volumes séparés sont reçus par le **Service de Vente des Éditions du Muséum** (pour la France et les DOM-TOM uniquement) ou par **Universal Book Services**. Catalogue sur demande. Une liste des derniers titres parus figure en page 3 de couverture.

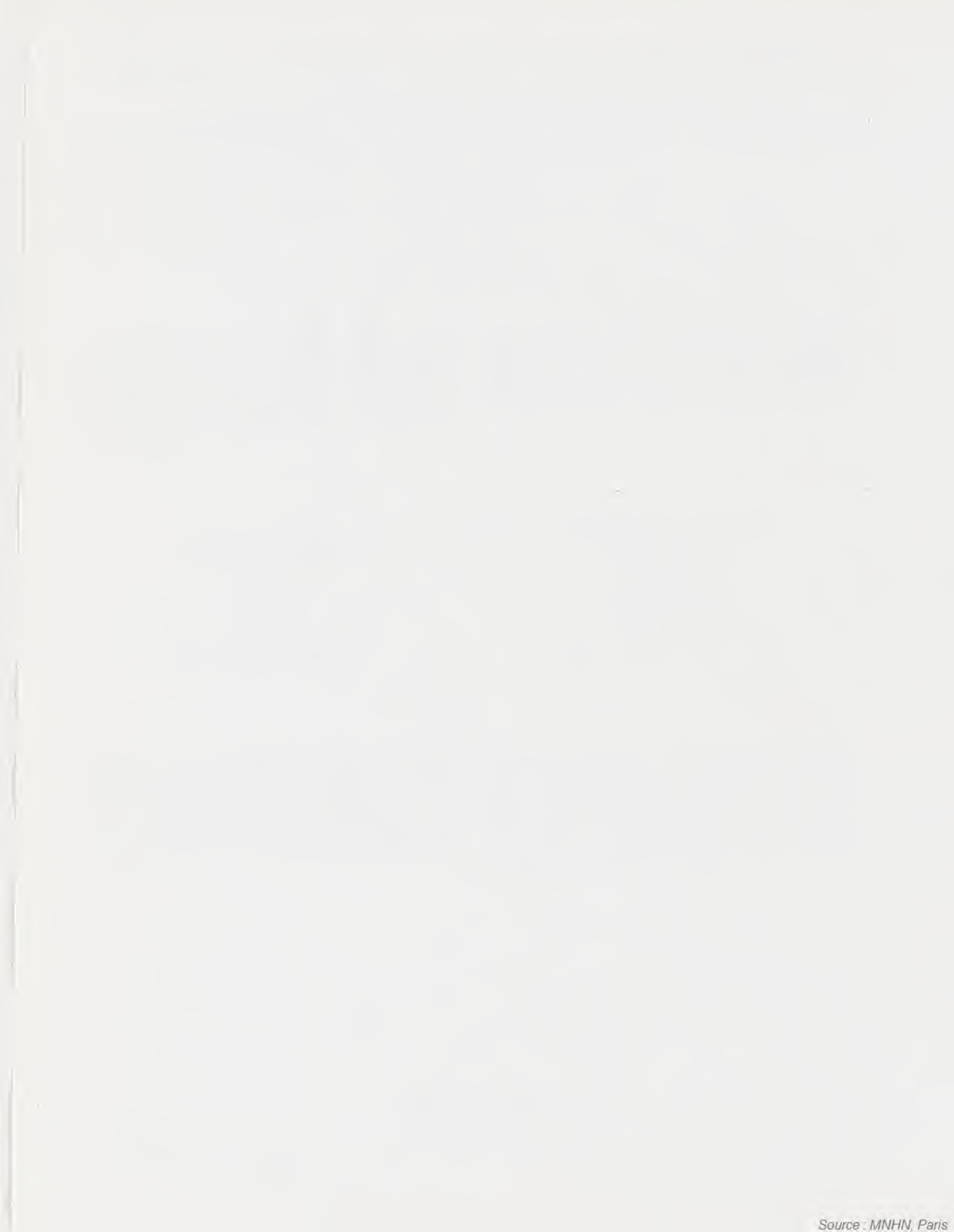
*Volumes are published at irregular intervals, and at irregular prices. Standing orders and orders for single volumes should be directed to the* ***Service de Vente des Éditions du Muséum*** *(for France and DOM-TOM only) or* ***Universal Book Services****. Free price list and catalogue are available on request. Recently published memoirs are listed on page 3 of the cover.*

*Printed on acid-free paper*
Imprimé sur papier non acide

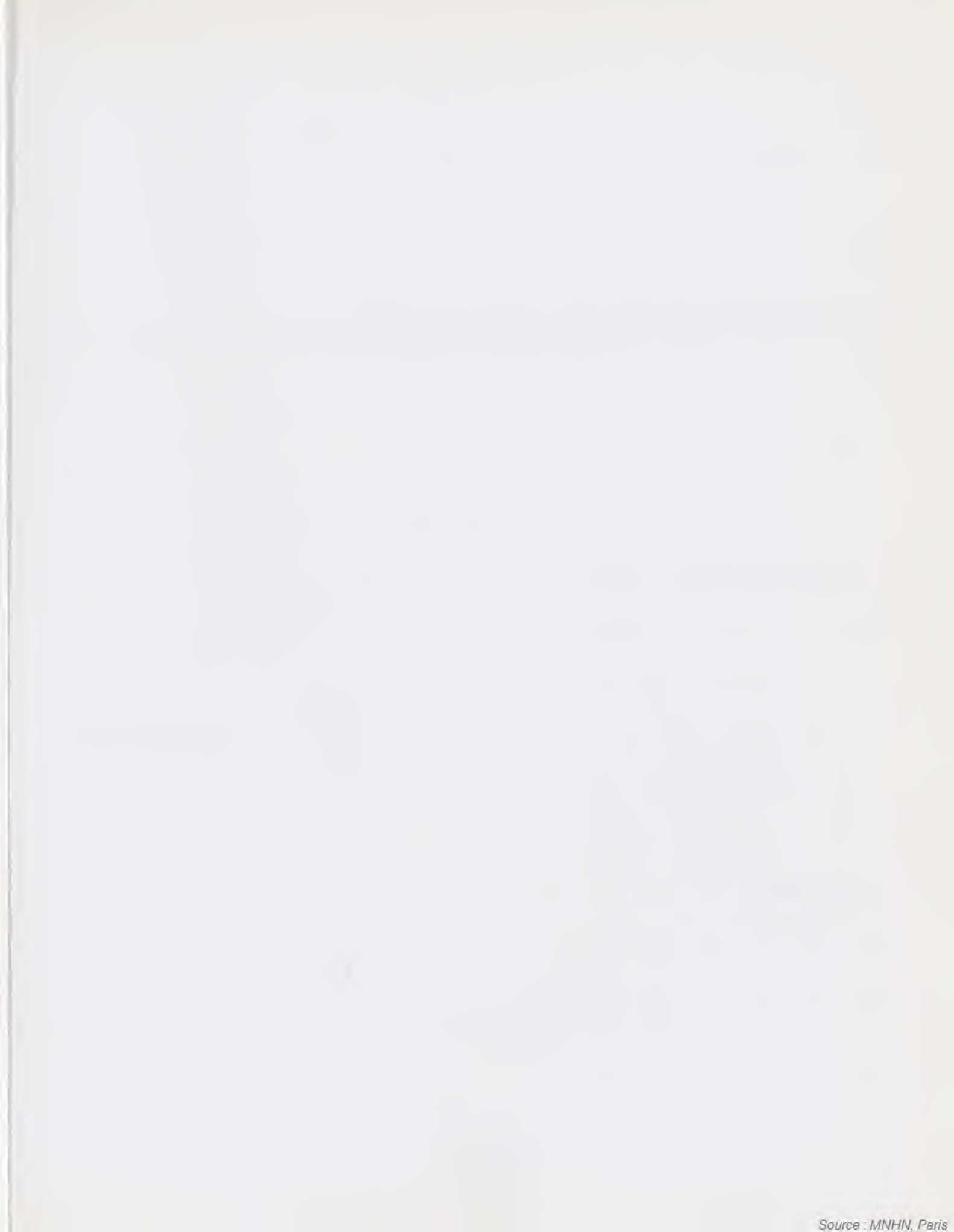
Source : MNHN, Paris

Bibliothèque Centrale Muséum
3 3001 00125984 4

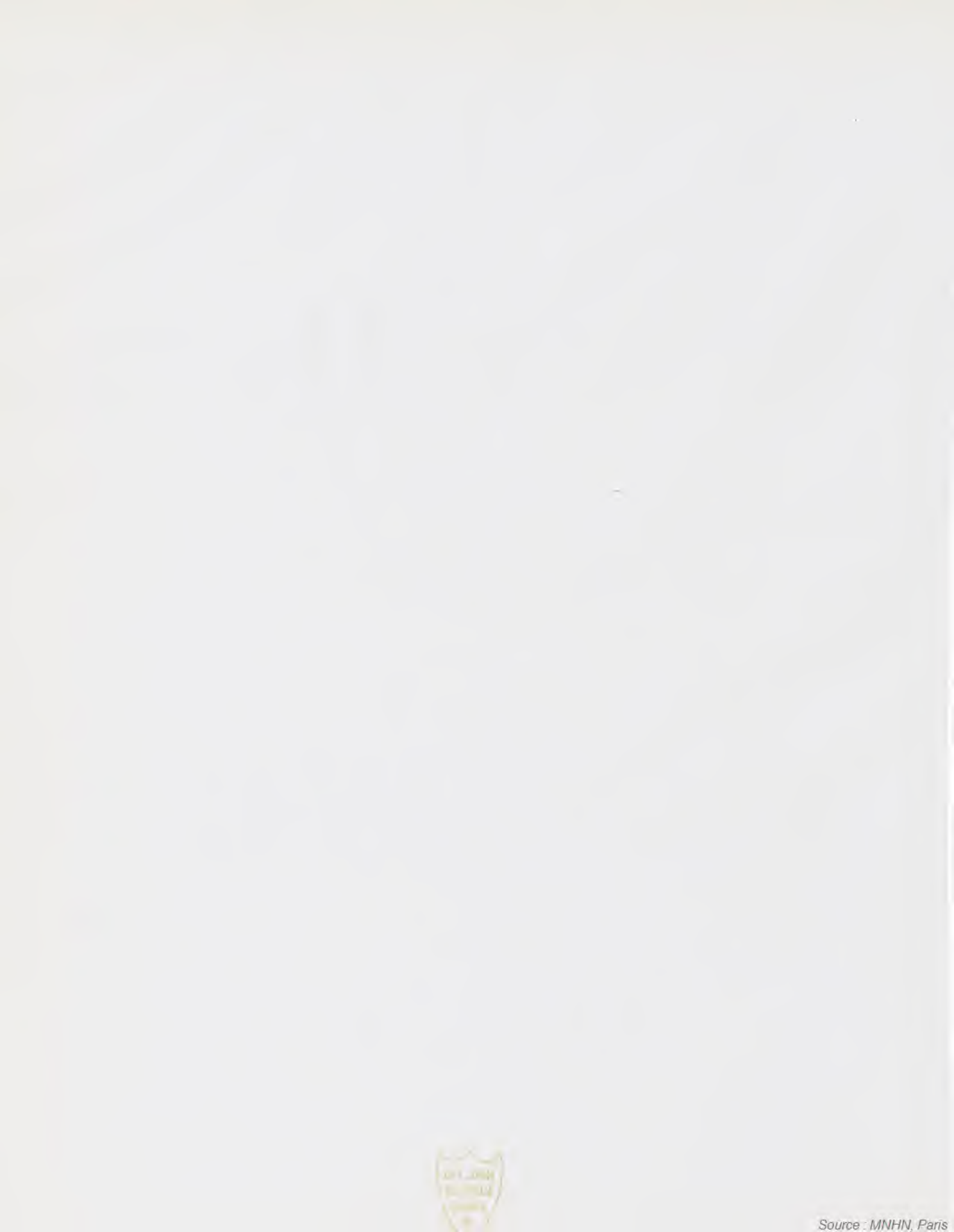
Source : MNHN, Paris



Source : MNHN, Paris



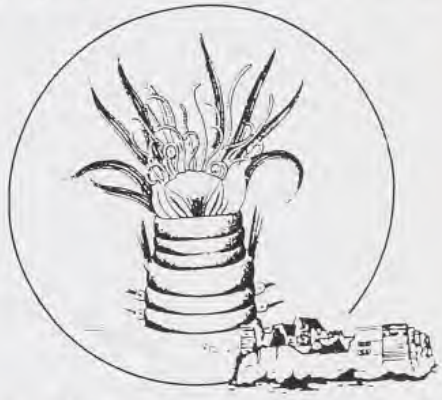
Source : MNHN, Paris



Source : MNHN, Paris

# *Actes de la 4ème Conférence internationale des Polychètes*

4TH INTERNATIONAL
POLYCHAETE
CONFERENCE



ANGERS
FRANCE
1992

BIBL. DU
MUSÉUM
PARIS

Source : MNHN, Paris

ISBN : 2-85653-214-4
ISSN : 1243-4442
© Éditions du Muséum national d'Histoire naturelle, Paris, 1994

PHOTOCOPIES :

Les *Mémoires du Muséum* adhèrent au Centre Français d'Exploitation du Droit de Copie (CFC), 3, rue Hautefeuille, 75006 Paris. Le CFC est membre de l'International Federation of Reproduction Rights Organisations (IFRRO). Aux États-Unis d'Amérique, contacter le Copyright Clearance Center, 27, Congress Street, Salem, Massachusetts 01970.

*PHOTOCOPIES :*

*The* Mémoires du Muséum *adhere to the Centre Français d'Exploitation du Droit de Copie (CFC), 3, rue Hautefeuille, 75006 Paris. The CFC is a member of International Federation of Reproduction Rights Organisations (IFRRO). In USA, contact the Copyright Clearance Center, 27, Congress Street, Salem, Massachusetts 01970.*

Source : MNHN, Paris

Fr. 260 C4
3ème Ex

MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

TOME 162
ZOOLOGIE

# *Actes de la 4ème Conférence internationale des Polychètes*

Jean-Claude DAUVIN* Lucien LAUBIER** Donald J. REISH***

* Muséum national d'Histoire naturelle
Laboratoire de Biologie des Invertébrés marins et Malacologie
57, rue Cuvier
F-75005 Paris

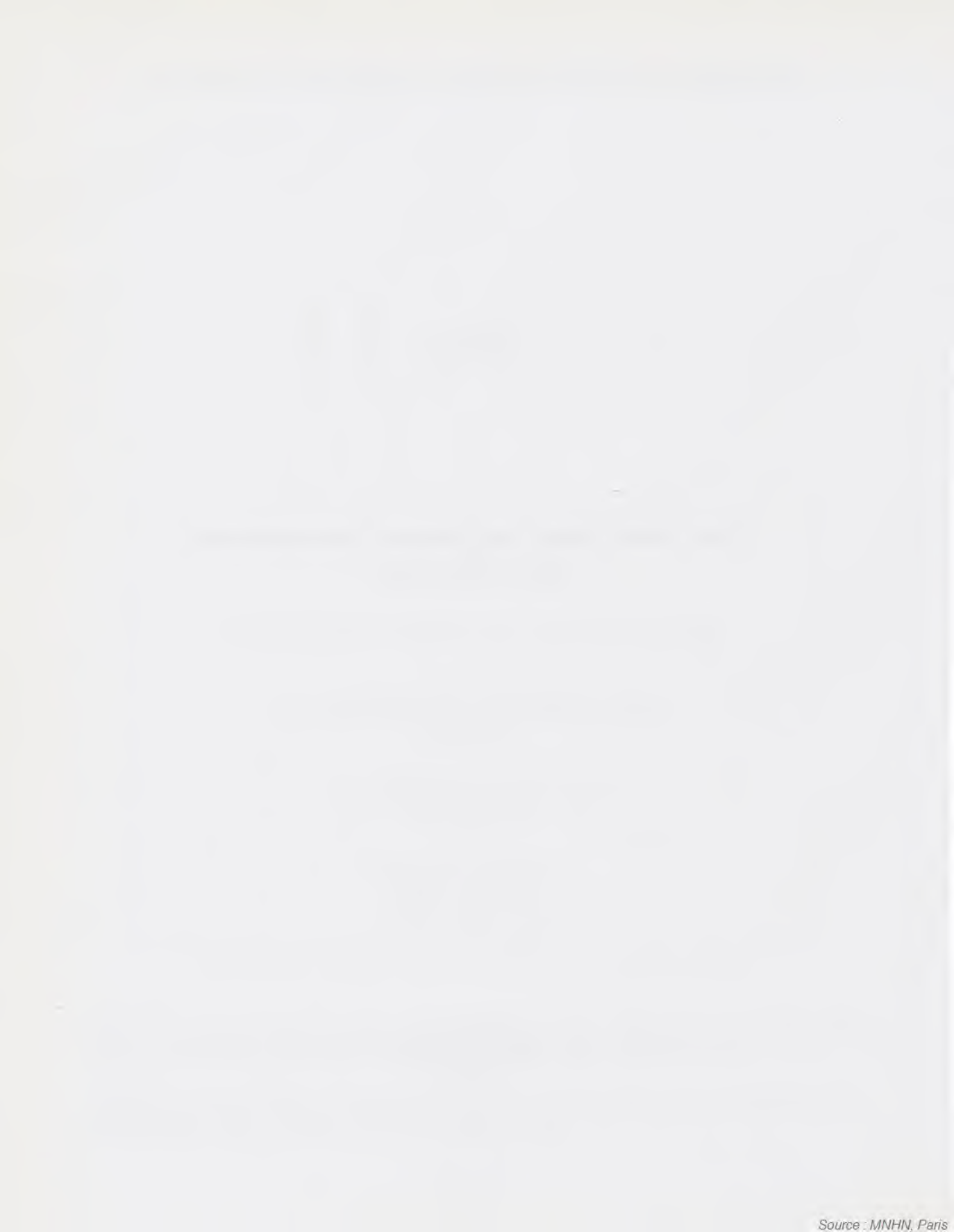
** Institut Océanographique
Laboratoire de Physiologie des Etres marins
195, rue Saint-Jacques
F-75005 Paris

*** California State University
Department of Biology
Long Beach, CA 90804
USA

ÉDITIONS
DU MUSÉUM
PARIS

1994

Source : MNHN, Paris



Source : MNHN, Paris

# CONTENTS

# SOMMAIRE


Preface ..... 9

Acknowledgements ..... 10

List of participants ..... 11

List of reviewers ..... 15

Obituaries ..... 17

Pierre FAUVEL ..... 17

Ralph I. SMITH ..... 19

Pavel V. USHAKOV ..... 19

Douglas P. WILSON ..... 22

Contributed papers ..... 25

Cytophysiology, development and reproduction ..... 29

Genetics and morphology ..... 81

Phylogeny and taxonomy ..... 145

Ecology and biogeography ..... 323

Culture and valorisation ..... 593

Abstracts ..... 611


Source : MNHN, Paris

Source : MNHN, Paris

# PREFACE

Some eight years ago, Professor KIRKEGAARD, former Chairman of the International Polychaete Association and organizer of the Second International Polychaete Conference, suggested that France, as a European southern country, should host the Fourth Conference. We fully agreed on this idea, and decided to prepare a proposal which was submitted to the Association during the Third International Polychaete Conference held in Long Beach, August 1989. At this time, one of our main difficulties was the choice of the site for this Conference. For several reasons, most of the french organizers considered the town of Angers as the most appropriate place: the souvenir of Pierre FAUVEL and of his successor François RULLIER, the availability of convenient facilities, the assistance of Patrick GILLET's laboratory in the Institute for Pure and Applied Research of the Université Catholique de l'Ouest, the opportunity for attendees to discover and copy rare articles and books from FAUVEL's library, the touristic interest of the surroundings of the town of Angers...

During the Long Beach Conference, the French proposal was presented together with two others proposals, and finally adopted by the Association. In accordance with the discussions in Long Beach, we decided to move the period of the Conference to the end of July instead of the beginning of September; we also considered the possibility to organize some sampling visits in French classical marine stations and kept in mind the idea of widening the scope of the Conference to physiology and endocrinology of Polychaetes. More generally, we followed one suggestion by David GEORGE: such an international Conference should not be restricted to ecology and taxonomy, but should also consider the group as a biological model, and include applied research such as zootechny for polychaete farming or search for active molecules such as nereidin or thelepin. The program of the Proceedings clearly demonstrates that this objective has been achieved.

Following the decision of the International Polychaete Association, an Organization Committee was soon established in France:

President of the Organization Committee: Lucien LAUBIER, Bruxelles

Convener: Patrick GILLET, Angers

Gérard BELLAN, Marseille
Michel BHAUD, Banyuls-sur-Mer
Jean-Claude DAUVIN, Paris
Daniel DESBRUYÈRES, Brest
André DHAINAUT, Lille
Nicole DHAINAUT-COURTOIS, Lille
Yves GRUET, Nantes
Christian RETIÈRE, Dinard
Jean VOVELLE, Paris

Local organization Committee, Université Catholique de l'Ouest, Angers:

Elisabeth AILLERIE, Georges LE GUILLANTON, and Anne-Laure MORVAN.

The first announcement was sent at the end of December, 1990. In May 1991, we had received 164 positive answers, 80 communications titles and 25 posters. A few weeks later, the same figures were respectively 190, 130 and 60.

The Fourth International Polychaete Conference was held July 27-August 1, 1992, at the Centre de Congrès, Angers, France. A total of 200 members from 32 countries attended the Conference. Sessions were conducted over

Source : MNHN, Paris

a six days period with two mid-excursions: to the Loire Valley and to Bourgneuf Bay. Several attendees traveled to the Laboratoire maritime de Dinard following the Conference.

There were 71 oral presentations and 101 posters. Session topics and posters represented the different themes: cytophysiology, taxonomy and phylogeny, biogeography and ecology, reproduction and development. A special session was organized on polychaete culture and valorisation. Seventy-nine papers were submitted for publication and analysed by two different reviewers, and by Donald J. REISH. A total of fourteen papers have been rejected by the reviewers, but abstracts of all communications and posters are included in the Proceedings of the Conference.

Lucien LAUBIER and Patrick GILLET

## ACKNOWLEDGEMENTS

We gratefully acknowledge the financial support and practical assistance to the Conference provided by the different ministries and various bodies and scientific institutions:

- Ministère des Affaires Etrangères
- Conseil Régional des Pays de la Loire
- Conseil Général du Maine et Loire
- Ville d'Angers
- Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER)
- Université Catholique de l'Ouest (UCO)
- Institut de Recherche Fondamentale et Appliquée de l'UCO
- Muséum National d'Histoire Naturelle de Paris,
- Muséum d'Histoire Naturelle de Nantes.

Special thanks for their help to Yves GRUET and Christian RETIÈRE who organized excursions, and to Elisabeth AILLERIE for the programme. Thanks are also extended to Marie-Annick GRUET, Marie-Hélène GILLET and Elisabeth AILLERIE for their kind assistance during the Conference.

Many thanks to the Minitextiles Art group for the exhibition on polychaetes.

A special mention must be addressed to the Laboratoire de Biologie des Invertébrés Marins et Malacologie du Muséum national d'Histoire naturelle, which provided logistic support during the tedious work of preparation of the present volume.

Source : MNHN, Paris

# LIST OF PARTICIPANTS

**ARGENTINA**

AMOR Analia (La Plata)
BREMEC Claudia (La Plata)

**AUSTRALIA**

HUTCHINGS Patricia (Sydney)

**BELGIUM**

EECKHAUT Igor (Mons)

**BRAZIL**

LANA Paulo Da Cunha (Parana)
NONATO Edmundo Ferraz (Sao Paulo)
SALVADOR BELLINTANI Lara (Sao Paulo)
SANTOS Maria Auxiadora (Sergipe)

**CANADA**

BYERS Sheila (Toronto)
CARON Alain (Dinard)
CHIA Fu-shiang (Alberta)
DESROSIERS Gaston (Rimouski)
FOURNIER Judith A. (Ottawa)
JUNIPER Kim (Montréal)
MARSDEN Joan (Montréal)
MASSON Stéphane (Québec)
MILLER RETZER Connie (Vancouver)
MIRON Gilles (Québec)
OLIVIER Marc (Rimouski)
POCKLINGTON Patricia (Halifax)
QIAN Pei-Yuan (Vancouver)
WHITE Caroline (Rimouski)

**COLOMBIA**

LAVERDE-CASTILLO Juan José Antonio (Bogota)

**CROATIA**

ZAHTILA Elvis (Rovinj)

**DENMARK**

EIBYE-JACOBSEN Danny (Copenhagen)
FELDSGAARD PEDERSEN Torben (Aarhus C.)
HYLLBERG Jorgen (Aarhus C.)
KIRKEGAARD Jorgen Bagger (Copenhagen)
PETERSEN Mary E. (Copenhagen)

**CHILE**

CARRASCO Franklin D. (Concepcion)

**CHINA**

WU Baoling (Qing Dao)

**FRANCE**

BACHELET Guy (Arcachon)
BAUDET Joseph (Nantes)
BELLAN Gérard (Marseille)
BELLAN-SANTINI Denise (Marseille)
BHAUD Michel (Banyuls-sur-Mer)
CHA Jae Hoon (Banyuls-sur-Mer)
DAUVIN Jean-Claude (Paris)
DESBRUYÈRES Daniel (Brest)
DHAINAUT André (Villeneuve d'Ascq)
DHAINAUT-COURTOIS Nicole (Villeneuve d'Ascq)
DUCHÊNE Jean-Claude (Banyuls-sur-Mer)
GENTIL Franck (Roscoff)
GILLET Patrick (Angers)
GRUET Yves (Nantes)
INTÈS André (Brest)
JOUIN-TOULMOND Claude (Paris)
LAMBERT Rémy (Dinard)
LAUBIER Lucien (Paris)
LECHAPT Jean-Paul (Dinard)
MARCANO Guillermo (Arcachon)
NOZAIS Christian (Banyuls-sur-Mer)
PARREIRA DOS SANTOS Paulo Jorge (Arcachon)
PEREIRA DE SOUZA SANTOS Lilia (Arcachon)
RETIÈRE Christian (Dinard)
SALEN-PICARD Chantal (Marseille)
THIÉBAUT Eric (Roscoff)
VOVELLE Jean (Paris)

**GERMANY**

BOROWSKI Christian (Hamburg)
DORRESTEIJN Adriaan (Mainz)

Source : MNHN, Paris

FIEGE Dieter (Frankfurt)
FISCHER Albrecht (Mainz)
GOERKE Helmut (Bremerhaven)
HARDEGE Jorg Detelf (Oldenburg)
HOFMANN Dieter K. (Bochum)
HUSEMANN Eginhard (Bochum)
LICHER Frank (Osnabruck)
PLATE Susanne (Bochum)
PURSCHKE Gunter (Osnabruck)
ROSENFELDT Pongchai (Hamburg)
SCHMIDT Hartmut (Osnabruck)
WESTHEIDE Wilfried (Osnabruck)
WINDOFFER Reinhard (Osnabruck)
WRZESINSKI Olgierd (Hamburg)

**GREECE**

ARVANITIDIS Christos (Thessaloniki)
ELEFTHERIOU Anastasios (Iraklio)
PAPADOPOULOU K. Nadia (Iraklio)
SIMBOURA Nomiki (Athènes)

**INDIA**

AYYAKKANNU K. (Parangipettai)

**INDONESIA**

ANDI Isdradjat S. (Aarhus C.)
ARIO Raden (Aarhus C.)
BONEKA Farnis B. (Aarhus C.)
ERLAMBANG Tanza (Aarhus C.)
KALIGIS G. Fontje (Aarhus C.)
LATAMA Gunarto (Aarhus C.)
LITAAY Magdalena (Aarhus C.)
OMPI Medy (Aarhus C.)
PRINGGENIES Delianis (Aarhus C.)
SIREGAR Yusni I. (Aarhus C.)
SOEKENDARSI Eddy (Aarhus C.)
TANJUNG Afrizal (Aarhus C.)
YULIANDA Fredinan (Aarhus C.)

**IRELAND**

ALLEN Hazel
GREHAN Anthony J. (Banyuls-sur-Mer)

**ISRAEL**

BEN-ELIAHU Nechama (Jerusalem)

**ITALY**

ABBIATI Marco (Pisa)
CANTONE Grazia (Catania)
CASTELLI Alberto (Modena)
GAMBI M. Cristina (Napoli)
GIANGRANDE Adriana (Lecce)
GRAVINA M. Flavia (Roma)
LARDICCI Claudio (Pisa)
PETRAPOLI Angela (Lecce)
PREVEDELLI Daniela (Modena)
SANFILIPPO Rossana (Catania)
SELLA Gabriella (Torino)
SOMASHINI Alessandra (Roma)
SORDINO Paolo (Napoli)

**JAPAN**

SATO-OKOSHI Waka (Sendai)

**MEXIQUE**

DIAZ Victoria (San Diego)
LEON GONZALEZ Jesus Angel de (N. Leon)
MOLINA-FUENTES Enrique (San Nicolas de los Garza)
SALAZAR-VALLEJO Sergio I. (Chetumal)
SOLIS-WEISS Vivianne (Mexico)

**NETHERLANDS**

HOVE Harry Ten (Amsterdam)

**NORWAY**

HOLTE Boerge (Tromsoe)
JORGENSEN Lis Lindal (Bergen)
OUG Eivind (Grimstad)

**POLAND**

SICINSKI Jacek (Todz)

**PORTUGAL**

MARQUES Joao Carlos (Coimbra)
MOREIRA Maria Helena (Aveiro)
PARDAL Miguel Angelo (Coimbra)
SILVA Paula Cristina (Aveiro)

**RUSSIA**

BRITAYEV Temir (Moscow)
JIRKOV Igor A. (Moscow)
TZETLIN Alexander (Moscow)

**SPAIN**

ALOS CALVO Maria Carmen (Barcelone)

Source : MNHN, Paris

BRITO Maria Carmen (La Laguna)
CAPACCIONI-AZZATI Romana Y. (Valencia)
CARDELL Maria José (Barcelone)
DUESO Ana (Blanes)
GARCIA-ARBERAS Loreto (Bilbao)
GARCIA-MARTIN Salvador F. (Puerto Real)
JUNOY Juan (Madrid)
LASTRA Mariano (Santiago)
LOPEZ GARCIA Eduardo (Madrid)
MENDEZ Muria (Barcelone)
NUNEZ Jorge (Islas Canarias)
PINEDO Susana (Blanes)
RALLO Ana (Bilbao)
SARDA Rafael (Blanes)
SANCHEZ MATA Adoracion (Santiago)
SAN MARTIN Guillermo (Madrid)
TENA MEDIALDEA Jose (Valencia)
TORRES GAVILA Franco Javier (Burjasso)
VIEITEZ Jose Manuel (Alcala de Henares)
VILLORA-MORENO Santiago (Valencia)

**SWEDEN**

ÅKESSON Bertil (Goteborg)
EIDE Ragnar (Goteborg)
PLEIJEL Fredrik (Stockholm)
SIGVALDADOTTIR Elin (Stockholm)

**TAIWAN**

CHEN Chang-Po (Taiwan)
HSIEH Hwey-Lian (Taipei)

**THAILAND**

CHANTRAPORNSYL Supot (Aarhus)
NATEEWATHANA Anuwat (Phuket)

**TRINIDAD**

GOBIN Judith (Plymouth)

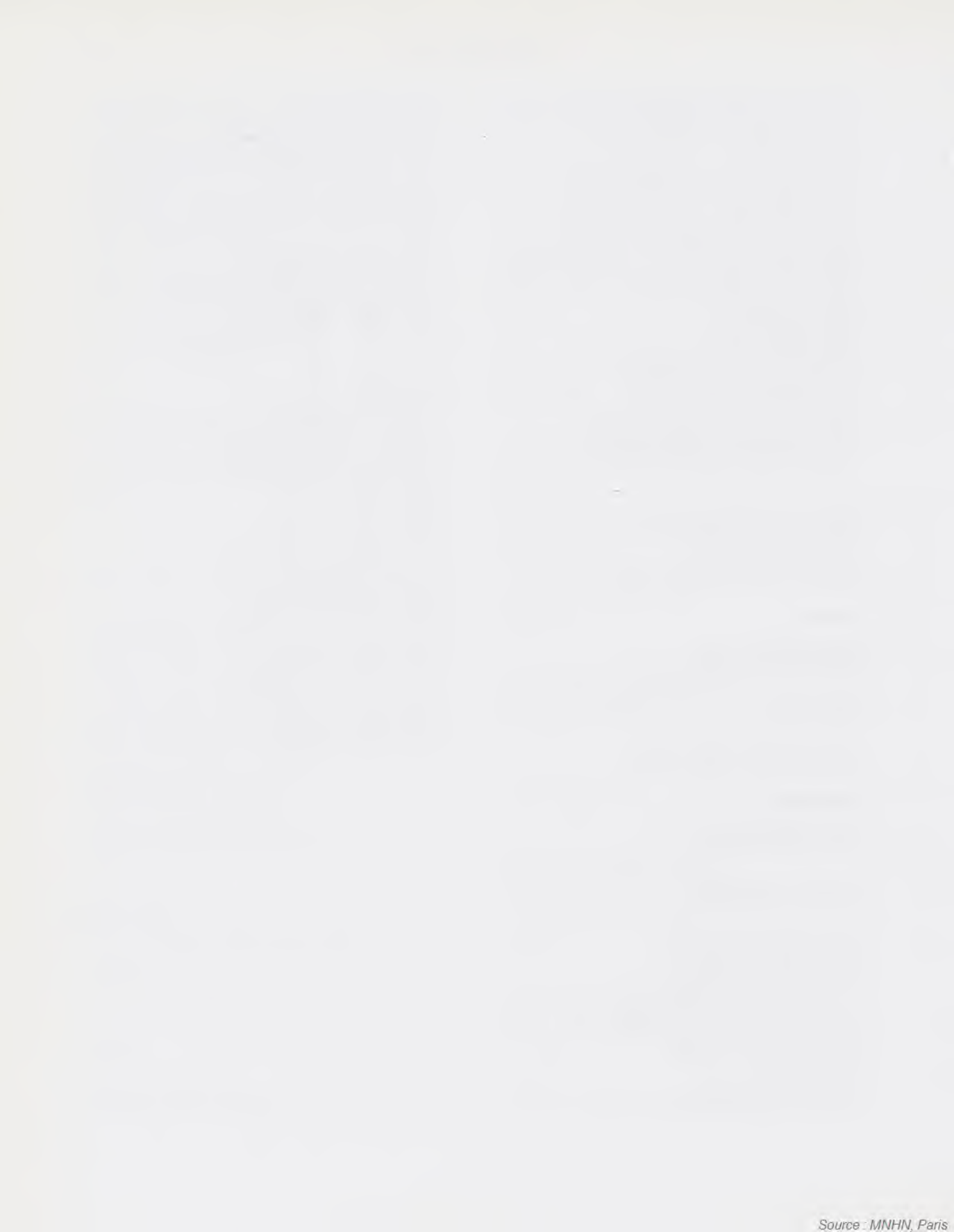
**UNITED KINGDOM**

BAMBER Roger (Southampton)
BATTEN Sonia (Southampton)
BENTLEY Matt (St Andrews)
CHAMBERS Susan (Edinburg)
COATES Amanda (Scotland)
CUNNINGHAM Elaine (Tyne and Wear)
DIXON David R. (Plymouth)
EMSON Roland H. (London)
GEORGE David (London)
GIBBS Peter E. (Plymouth)
HARRIS Tegwyn (Exeter)
KENDALL Michael (Plymouth)
KNIGHT-JONES Phyllis (Swansea)
KNIGHT-JONES Wyn (Swansea)
MACKIE Andrew (Wales)
MUIR Alexander Ian (London)
OLIVE Peter James William (Tyne)
PATERSON Gordon L. J. (London)
ROWE Grant (Southampton)
THORP Clifford H. (Hampshire)
TURNER Geoffrey Simon (Tyne and Wear)
WARREN Lynda (Cardiff)
WOODHAM Annette (Edinburgh)

**UNITED STATES OF AMERICA**

BLAKE James A. (Woods Hole)
DAUER Daniel (Norfolk)
FAUCHALD Kristian (Washington)
FITZHUGH Kirk (Los Angeles)
HILBIG Brigitte (Massachusetts)
JONES Howard (Corvallis)
KIRTLEY David W. (Stuart)
KUDENOV Jerry D. (Alaska)
LONG Charlene D.
LOVELL Lawrence L. (California)
MAC HUGH Damhnait (Santa Cruz)
MARTIN Ann (Redondo Beach)
MOUNTFORD Nancy K. (Lusby)
REISH Donald J. (Long Beach)
ROUSE Greg (Washington)
RUFF R. Eugene (Needham)
SCHROEDER Paul C. (Pullmann)
SIMON Joseph L. (Tampa)
SMITH Ralph I. (Berkeley)
WARD Linda (Washington)

Source : MNHN, Paris



Source : MNHN, Paris

# LIST OF REVIEWERS

## AUSTRALIA

GLASBY Chris (Canberra)
HUTCHINGS Patricia (Sydney)
PAXTON Hannelore (North Ryde)
WILSON Robin (Victoria)

## BRAZIL

LANA Paulo Da Cunha (Parana)

## CANADA

FOURNIER Judith A. (Ottawa)
POCKLINGTON Patricia (Halifax)

## COLOMBIA

LAVERDE-CASTILLO Juan José Antonio (Bogota)

## DENMARK

EIBYE-JACOBSEN Danny (Copenhagen)
PETERSEN Mary E. (Copenhagen)

## FRANCE

AMIARD Jean-Claude (Nantes)
BACHELET Guy (Arcachon)
BELLAN Gérard (Marseille)
BHAUD Michel (Banyuls-sur-Mer)
DAUVIN Jean-Claude (Paris)
DESBRUYÈRES Daniel (Brest)
DHAINAUT André (Villeneuve d'Ascq)
DUCHÊNE Jean-Claude (Banyuls-sur-Mer)
GENTIL Franck (Roscoff)
GILLET Patrick (Angers)
GLÉMAREC Michel (Brest)
GRUET Yves (Nantes)
JOUIN-TOULMOND Claude (Paris)
LAUBIER Lucien (Paris)
PEYROT-CLAUSADE Mireille (Marseille)
RETIÈRE Christian (Dinard)
SIBUET Myriam (Brest)
TOULMOND André (Paris)
VOVELLE Jean (Paris)
ZIBROWIUS Helmut (Marseille)

## GERMANY

DORRESTEIJN Adriaan (Mainz)
FISCHER Albrecht (Mainz)
GOERKE Helmut (Bremerhaven)
HARDEGE Jorg Detelf (Oldenburg)
PURSCHKE Gunter (Osnabruck)
WESTHEIDE Wilfried (Osnabruck)

## ISRAEL

BEN-ELIAHU Nechama (Jerusalem)

## ITALY

CASTELLI Alberto (Modena)
GAMBI M. Cristina (Napoli)
GIANGRANDE Adriana (Lecce)

## NETHERLANDS

HOVE Harry Ten (Amsterdam)

## NORWAY

HOLTE Boerge (Tromsoe)

## SPAIN

SARDA Rafael (Blanes)
SAN MARTIN Guillermo (Madrid)

## SWEDEN

ÅKESSON Bertil (Goteborg)
PLEIJEL Fredrik (Stockholm)
SIGVALDADOTTIR Elin (Stockholm)

## UNITED KINGDOM

GEORGE David (London)
GIBBS Peter E. (Plymouth)
KENDALL Michael (Plymouth)
KNIGHT-JONES Phyllis (Swansea)
KNIGHT-JONES Wyn (Swansea)
MACKIE Andrew (Wales)
METTAM Chris (Cardiff)
MUIR Alexander Ian (London)

Source : MNHN, Paris

OLIVE Peter James William (Tyne)
PATERSON Gordon L.J. (London)
WARREN Lynda (Cardiff)

## UNITED STATES OF AMERICA

BLAKE James A. (Woods Hole)
BUTMAN Cheryl Ann (Woods Hole)
FAUCHALD Kristian (Washington)
FITZHUGH Kirk (Los Angeles)
GRASSLE Frederick (New Brunswick)
GRASSLE Judith (New Brunswick)
HILBIG Brigitte (Massachusetts)
KUDENOV Jerry D. (Alaska)
LEVIN Lisa A. (La Jolla)
MAURER Don (Long Beach)
PERKINS Thomas H. (St Petersburg)
PETTIBONE Marian H. (Washington)
REISH Donald J. (Long Beach)
ROUSE Greg (Washington)
SCHROEDER Paul C. (Pullmann)
SIMON Joseph L. (Tampa)

Source : MNHN, Paris

# Obituaries

## Pierre FAUVEL (1866-1958), his life and research on polychaetous annelids

Patrick GILLET

Laboratoire d'Ecologie Animale
Institut de Recherche Fondamentale et Appliquée
Université Catholique de l'Ouest
3, place André Leroy, B.P. 808
49008 Angers cedex 01, France

Pierre Louis André FAUVEL (Fig. 1) est né à Cherbourg le 8 octobre 1866 de Clémence Mathilde CAPPE (1851-1909) et de Auguste Alexandre FAUVEL (1821-1867), lieutenant dans la marine française. Pierre FAUVEL a suivi ses études à l'Université de Caen et fut assistant à la station de recherche de Luc-sur-Mer. Le 29 juin 1897, il obtint son doctorat à l'Université de Paris pour son travail sur les Ampharétiens. Il fut alors nommé professeur de zoologie à l'Université Catholique de l'Ouest, puis Doyen de la Faculté des Sciences en 1942.

Il étudia les polychètes de différentes régions du monde et de nombreuses expéditions océanographiques telles que celles de l'Hirondelle, de la Princesse Alice, du Pourquoi Pas ? et de la Calypso. Il découvrit de nombreuses espèces nouvelles dont la plus célèbre est *Mercierella enigmatica* découverte dans le canal de Caen par M. MERCIER. Pierre FAUVEL avait remarqué les analogies avec *Ficopomatus macrodon* et ce n'est que récemment que l'espèce fut rebaptisée *Ficopomatus enigmaticus* par TEN HOVE & WERDENBURG (1978).

Il a publié environ 170 articles sur les annélides polychètes et rédigé de nombreuses faunes comme la Faune de France et la Faune de l'Inde. Ses travaux les plus importants ont porté sur l'anatomie comparée des Arénicoles, sur les otocystes, l'éthologie des Pectinaires et une monographie sur les Ampharétiens. Il obtint de nombreux prix et distinctions dont le Prix Savigny (1915) de l'Académie des Sciences, le Prix Saintour (1926) de l'Académie des Sciences, et le Prix Gadeau de Kerville (1930), de la Société Zoologique de France.

Pierre FAUVEL fit également des recherches de physiologie et de diététique humaine. Il publia une quarantaine d'articles sur le régime végétarien, la valeur alimentaire des différents pains et l'excrétion urique. Sous le pseudonyme d'Hollow-Rim, il signa également une trentaine d'articles sur le cyclisme. Pierre FAUVEL mourut le 12 décembre 1958 à l'âge de 92 ans. Comme l'écrivait P. USHAKOV le 4 mars 1959 à F. RULLIER. "Pierre FAUVEL fut un savant éminent qui a tant fait pour la connaissance des Polychètes. Les magnifiques œuvres du professeur FAUVEL nous ont servi à tous dans nos études comme exemple de recherches taxonomiques".

Pierre Louis André FAUVEL (Fig. 1) was born in Cherbourg in 1866 of Clémence Mathilde CAPPE (1851-1909) and of Auguste Alexandre FAUVEL (1821-1867) lieutenant in the French Marine. He was a student of biology at the University of Caen and became an assistant at the Luc-sur-Mer research station. On June 29, 1897 he passed his doctorate at the University of Paris for his work on Ampharetidae. He was then appointed Professor of Zoology at the Université Catholique de l'Ouest, and later Dean of the Faculty of Sciences. He studied polychaetes from different parts of the world and many expeditions such as Hirondelle, Princesse Alice, Pourquoi-Pas ? and Calypso. He found numerous new species but the most famous of all is *Mercierella (Ficopomatus) enigmatica* discovered in the Channel of Caen by M. MERCIER. He had written many fauna such as the Faune de France, the Fauna of India and won numerous prizes and distinctions including the Savigny Prize (1915), the

Source : MNHN, Paris

Saintour Prize (1926) from the Academy of Sciences and the Gadeau de Kerville Prize (1930) from the Société Zoologique de France. Pierre FAUVEL died on December 12, 1958, and François RULLIER (1907-1981) succeeded him in the laboratory.

FIG. 1. — Pierre FAUVEL au début du siècle

## RÉFÉRENCES


ANONYME. — *Cinquante années d'enseignement à l'Université Catholique d'Angers (1897-1947). M. Pierre Fauvel, Doyen de la Faculté des Sciences*. Editions de l'Ouest, Angers, 31 pp.

FAGE L., 1959. — Pierre Fauvel, 1866-1958. *Bull. Mus. nat. Hist. nat., Paris*, 2e sér., **31** : 1.

FAUVEL P., 1898. — Recherches sur les Ampharetidae. *Bull. Scient. France Belgique*, **30** : 277-489.

FAUVEL P., 1922. — Un nouveau Serpulien d'eau saumâtre (*Mercierella* n. g. *enigmatica* n. sp). *Bull. Soc. Zool. France*, **48** : 424-430.

GILLET P., 1992. — Travaux de Pierre Fauvel, François Rullier et Louis Amoureux sur les Annélides Polychètes de 1894 à 1985. *Bull. Soc. Sc. Nat. Ouest de la France*, **14** : 20-36.

RULLIER F., 1959. — M. le Doyen Pierre Fauvel. *Rev. Fac. Cath. Ouest*, **2** : 5-27.

TEN HOVE H., & J.C.A. WERDENBURG, 1978. — A generic revision of the brackish-water serpulid *Ficopomatus* Southern, 1921 (Polychaeta: Serpulidae) including *Mercierella* Fauvel, 1923, *Sphaeropomatus* Treadwell, 1934, *Mercierellopsis* Rioja, 1945 and *Neopomatus* Pilai, 1960. *Biol. Bull.*, **154** : 96-120.


Source : MNHN, Paris

## Ralph Ingram SMITH
## 1916-1993

Donald J. REISH

Department of Biology
California State University
Long Beach, California 90840, États-Unis

Ralph I. SMITH, professor Emeritus of Zoology at the University of California at Berkeley, died on May 12, 1993 in Santa Rosa, California. He collapsed after completing The Human Race; he was revived by emergency workers, but died a few days later. Professionally he was particularly interested in the physiological adaptations of intertidal invertebrates including polychaetes.

Ralph was born in Braintree, Massachusetts, on July 3, 1916. He attended Harvard University where he received his doctorate in 1942 under the direction of John Henry WALSH. Following service in the United States Army during World War II, he joined the faculty of the Zoology Department at the University of California at Berkeley, a position he held for 41 years until his retirement in 1987. During his tenure at UC Berkeley he served a term as department chairman, played a major role in the establishment of the University of California's Bodega Marine Laboratory, and directed 22 doctoral students.

Ralph emphatically denied being a systematist by any stretch of imagination, but he realized the importance of systematics. He believed in the importance of knowing and using the correct name of an organism. His interests in this is evident in his taking over Light's Manual (Intertidal Invertebrates of the Central California Coast) following the death of Dr. S. F. LIGHT. Later he organized and assembled a similar manual for the Woods Hole region where is often taught in the summer.

His contributions to the knowledge of polychaetes included developmental studies in the nereids and more recently in the terebellids. He published many papers on salinity tolerance and chloride regulation in nereids which was based not only with California species but European species as well. He attended the Third and Fourth International Polychaete Conferences and contributed papers to both.

His wife Todd of 52 years accompanied Ralph in their many travels which included visiting six continents. In addition to his wife, he is survived by two sisters, five children, and grandchildren.

## Pavel Vladimirovitch USHAKOV
## 1903-1992

Galina BUZHINSKAJA

Zoological Institute
Russian Academy of Sciences
St. Petersburg, Russia

On 25 February 1992, Dr. Professor Pavel Vladimirovitch USHAKOV passed away at the age of 88 of cardiac deficiency in the House of Science Veterans, Pushkin town, St. Petersburg.

The scope of scientific activity of Prof. P.V. USHAKOV included three fields of knowledge: zoology, marine biology and oceanography. He published about 250 scientific works; eighty of them, including three monographs, deal with systematics and phylogeny of polychaetes. He organized and participated in many marine expeditions

Source : MNHN, Paris

covering many different regions of the world's oceans, from the Arctic to the Antarctic Regions. He organized two marine biological stations in the USSR. His works were widely recognized throughout the world. Scientists of Australia, UK, USSR, USA, France, Germany, Sri-Lanka, named fifty-five marine organisms after him, i.e. algae, invertebrates and fishes.

He received the degree of Honoris Causa from Aix-Marseilles II University. In 1972, the Oceanographic Institute in Paris awarded him the Medal of Prince Albert I of Monaco, its highest international award, for his works on marine biology. The USSR Geographic Society awarded him the Semenov-Tienshansky Gold Medal in 1958 for his works on the Sea of Okhotsk. The USSR Academy of Sciences awarded him the Pavlovsky Gold Medal in 1983 for his studies of polychaetes.

P.V. USHAKOV was born on 27 June 1903 in St. Petersburg into a family of a lawyer. After finishing a gymnasium in 1920, he entered the Biological Department of the Physico-Mathematicae Faculty of Petrograd University. He began his marine biological research as a student in 1921. Together with two young scientists E.K. GURYANOVA and I.G. ZAKS, he studied bionomy of the intertidal zone of Kola Bay and seasonal variations of its like. This study became a classical work and was widely recognized by marine biologists.

After graduation from the University, USHAKOV worked from 1924-1934 in the State Hydrological Institute, first as a technician, then as a scientist in the Hydrobiology Department. During 1923-1926, USHAKOV headed small research teams on the Novaya Zemlya islands where they studied coastal marine fauna and fauna of relict lakes. Until 1935, he took part in different expeditions to the White, Barents, Chuckchee, Okhotsk and Japan Seas. These expeditions resulted in a number of works including the volumes "Fauna and flora of the Chuckchee Sea" (1952) published on the initiative and under the editorship of P.V. USHAKOV and "The Fauna of the Sea of Okhotsk and conditions of its existence" (1953). It was in the Sea of Okhotsk that USHAKOV, then on board the trawler "Gagara", recovered the first-ever animal specimen from a depth of more than 3,000 m. Among them were hitherto unknown animals for which the new phylum Pogonophora was later erected.

Based on the study of flora and fauna of the Sea of Okhotsk he suggested for the first time a scheme of vertical zonation of the sea and showed that the Sea of Okhotsk and the Pacific Ocean were connected at depth via the straits between the islands making up the Kuril Island Arc.

In 1931, he organized Kamchatka Marine Station in Avachinskaya Bay. In 1933, he received the degree of Doctor of Biological Sciences. From 1936 to 1939, he organized Murmansk Biological Station of the USSR Academy of Sciences in Dalniye Zelentsy and developed investigations there. In 1939, he returned to the State Hydrological Institute. He supervised and participated in preparing hydrological manuals on the Okhotsk and Bering seas. During World War II, P.V. USHAKOV was in military service in the rank of engineer major and worked on hydrometeorological manuals for the Navy.

From 1946 to 1982 P.V. USHAKOV worked at the Zoological Institute of the USSR Academy of Sciences (Leningrad). He was the head of the Laboratory of Marine Research of the Institute until 1966. Then he became Curator of the Department of Annelids and Bryozoans. At that period, he focused on marine fauna, ecology and biogeography, systematics and phylogeny of polychaetes. In 1948, he participated in the Kuril-Sakhalin expedition of the Zoological Institute and Pacific Institute of Fisheries and Oceanography on board the "Toporok" research vessel. Material of this expedition formed an important part of his book "Polychaetes of the Far Eastern Seas of the USSR" (1955). In 1949, he took part in the first Pacific voyage of the "Vitiaz" research vessel and conducted trawling in the Kuril-Kamchatka trench, when bottom-dwelling animals were recovered from a depth of more than 8,000 m for the first time. In 1950 he published "Polychaetes of the Sea of Okhotsk". In 1956, he participated in the first Soviet Antarctic Expedition on the research vessel "Ob". As a result of the expedition, he published a number of papers dealing with quantitative distribution of benthos in Antarctic waters, patterns of vertical distribution of biocoenoses of bottom fauna and with systematics of Antarctic polychaetes. In 1957 and 1958, he worked on the Yellow and South China seas. In 1963, he conducted biological studies in Gulf of Guinea. P.V. USHAKOV visited France several times where he lectured in Marseilles University and in Sorbonne (Paris University). In 1965, he published "Polychaeta Errantia of the Yellow Sea" with WU Baoling. In 1972, he published his monograph "Polychaetes of the suborder Phyllodociformia of the Polar Basin and the north-western part of the Pacific" and in 1982 "Polychaetes of the suborder Aphroditiformia of the Arctic Ocean and the north-western part of the Pacific".

During the last 10 years P.V. USHAKOV lived in Pushkkin town in the House of Science Veterans where he wrote papers and essays on the history of science, memoirs about fellow scientists, i.e., his friends and contemporaries. His colleagues and disciples visited him regularly to discuss with him results of their studies and new initiatives.

Everyone who was fortunate enough to work and meet with P.V. USHAKOV will keep fond memories of him.

Source : MNHN, Paris

# Some personal souvenirs of P.V. USHAKOV

Lucien LAUBIER

Institut Océanographique
195, rue Saint-Jacques
75005 Paris, France

Since the Long Beach Conference, some famous polychaetologists have disappeared. Among others, I am thinking of Professor David DEAN, Professor Pavel Vladimirovitch USHAKOV and Professor Douglas P. WILSON. The death of P.V. USHAKOV, at the beginning of this year, was particularly sad for me and I would like to recall with his friends and colleagues a few souvenirs of the different visits he made in France.

I first met P.V. USKHAKOV in Summer 1965. He came from Marseilles to my laboratory in Banyuls-sur-Mer and spent a few days there. I remember a one day trip to the Spanish boarder, at a small village called Le Perthus. P.V. USHAKOV was astonished to discover that he, a citizen from the USSR, could walk through the custom freely, from France to Spain and back, without any inquiry from the french and spanish guards. On the same day, P.V. USHAKOV experienced the french way of eating snails, and found them just delicious. At the end of this visit, I took him with my car from Banyuls-sur-Mer to Angers: I had a rather fast car, a Citroën DS 19, and speed limitations were not a major problem for me. P.V. USHAKOV remained very quiet at 100 miles per hour, but I found later on that this journey became one of his frequent story when speaking of our relationship with other people ! We reached Angers without any trouble, and P.V. USHAKOV worked a few days with François RULLIER.

When the Second Oceanographic Congress took place in Moscow, in 1966, I attended the Congress and I had the opportunity to make a one day trip in Leningrad, now Saint Petersburg. P.V. USHAKOV invited me with Professor M. FONTAINE for a tea party in his small flat, where he lived with his daughter in law.

P.V. USHAKOV came back to Banyuls-sur-Mer in the Winter 1967-68, and spent a full fortnight working on Mediterranean Polychaetes. We went at sea together on board the small trawler Nereis, and P.V. USHAKOV was specially interested by a one meter long *Eunice rousseaui* living in a special glass-tube whick I kept for more than six years in my laboratory and exhibited during the easter and summer courses to the students. The regular wave along the body of the movement of the pectinate branchiae was fascinating... P.V. USHAKOV asked me for a posterior part of the worm, which I knew regenerated easily, and I gave him some 300 segments of this large Mediterranean *Eunice* which quickly recovered. During that visit, we had a party in my flat for Christmas night: we were all very surprised when P.V. USHAKOV quietly asked us about midnight Christmas mass: do French people usually go to church for Christmas mass? Moreover, he decided he wanted to go to church himself, where he attended the whole office.

When I moved to Brest, beginning of 1969. It was more difficult to wellcome P.V. USHAKOV in my next laboratory, due to the fact that Brest is also our main naval base for nuclear submarines... Nevertheless, I obtained that P.V. USHAKOV could come for two days under special permission. We had a long discussion about the 1917 Revolution, and P.V. USHAKOV told me that he very clearly saw the shots of the cruiser Aurora of the Winter Palace in Leningrad. At that time, I was working on deep-sea Mediterranean Polychaetes collected in the Hellenic Trench. I was specially interested by an aberrant tiny worm combining spiomorph and terebellomorph features. P.V. USHAKOV agreed on the fact that it should be described as a new genus. In fact, I described it as *Ushakovius enigmaticus*, type of a new sub-family, and Professor M. FONTAINE told P.V. USHAKOV of this new child when he gave to Professor USHAKOV the Manlay-Bendall medal of the Institut Océanographique in Paris, a few weeks after his visit to Brest. A few days later, P.V. USHAKOV told me that it should constitute a new family, which in fact was recently proposed by B. HOLTE.

Later on, P.V. USHAKOV retired from the Zoological Institute, I had no more opportunity to visit USSR, and I received some news exchanging letters with him. He of course wrote in French. Finally, Marina DOLGOLENKO was our last link.

I am sure all those who have had the chance to met P.V. USHAKOV and experienced his happiness will share my deep sadness.

Source : MNHN, Paris

# Douglas P. WILSON 1902-1991

David GEORGE

Department of Zoology
Natural History Museum
Cromwell Road
London, SW7 5BD, Royaume Uni

Dr. Douglas P. WILSON died suddenly on 18 December 1991 aged 89. "DP", as he colleagues, was born in Manchester and educated at William Hulme's Grammar School. After leaving school he started on a career in the Lancashire cotton industry, but this career was cut short by a dramatic slump in the cotton trade. Having from a very early age been keenly interested in natural history (particularly aquatic life) he decided to attend evening classes in zoology at Manchester University and also joined the Manchester Microscopical Society. This led to him doing practical work on the shore and to a decision that a career in zoology offered him a better life than a career in business. Consequently he enrolled in 1923 on a BSc course in zoology at Manchester University during which time he attended marine biology courses at Millport, Port Erin and Plymouth. Having gained a first class degree he obtained a grant in September 1926 to study polychaete development at the Marine Biological Association's laboratory at Plymouth, where less than a year and a half later, he was appointed to the staff as Assistant Naturalist with special responsibility for development of the public aquarium. DP remained at this marine station for the rest of his working life, officially over 10 years as Deputy Director, although continuing to work there until the end of 1981. From the start of his career at the laboratory until the beginning of the second world war, D.P. studied in detail the early development of polychaetes of many different families. His ability to rear polychaete larvae in the laboratory combined with his skills as a microscopist and a keen eye for detail contributed in no small measure to the scientific accuracy of his early research publications.

During the 1930's he began to investigate the influence of the substratum on the metamorphosis of larvae of such species as *Scolecolepis fuliginosa* and *Notomastus latericeus*, but unfortunately the war years and more applied research intervened. The Plymouth laboratory had cause to be grateful to DP during the second world war because it was his team of fire-fighters that saved the majority of the building by putting out the fires started by incendiary bombs dropped during an air raid.

After the war he returned to his work on habitat selection by metamorphosing larvae and produced a series of papers using mainly *Ophelia bicornis* as his experimental animal. He was able to show that larval settlement could be delayed for some considerable time if the substratum was not suitable, and that micro-organisms played an important role in making the substratum attractive to larvae. In 1951 he was awarded the Prix George KOHN, an award of the Institut Océanographique, Paris for a summary paper on this research. He had by this time obtained his DSc from Manchester University for his investigations on the early development of polychaetes.

In parallel with this work, and continuing until the late 1950's, DP conducted an interesting series of experiments on the "quality" of seawater in collaboration with a chemist at the laboratory, F.A.J. ARMSTRONG. Using sea urchin larvae he was able to show that larval development took place at different speeds and with varying degrees of success in seawater from different areas. In effect he had discovered a biological method for distinguishing seawaters of different origins, which effectively complemented the plankton indicator species concept developed by colleagues at the laboratory.

He next turned his attention to the biology of British species of magelonid and in the process uncovered some taxonomic problems which he solved by erecting two new *Magelona* species in the late 1950's. Interestingly his last scientific publication in 1982 returned once again to the genus, describing the larval development of three species from localities near Plymouth and Salcombe. However, most of DP's later contributions to the study of polychaetes dealt with British species of the Sabellariidae, the larvae of which he described in one of his earliest papers in 1929.

Soon after he recommenced work on the sabellariids the "Torrey Canyon" oil-tanker disaster occurred and he was able to use larvae of *Sabellaria spinulosa* to assess the long-term effects of low concentrations of the detergent used to clean up the oil. He followed this by studies on the early development of the reef-building shore-dwelling honeycomb worm *Sabellaria alveolata* and combined the laboratory work with valuable long-term monitoring of

Source : MNHN, Paris

recruitment and succession in colonies of the worm at Duckpool in north Cornwall from the early 1960's through to the mid 1970's. He showed that the larvae could delay metmorphosis, sometimes for many weeks, until a suitable substratum was found, and that they settled in preference on or near tubes of the same species, being attracted primarily by the chemical composition of the cement binding the sand grains of the tubes together. During these studies he made extensive use of photography to record not only the morphology of the developing larvae but also the changes in the shore colonies with time.

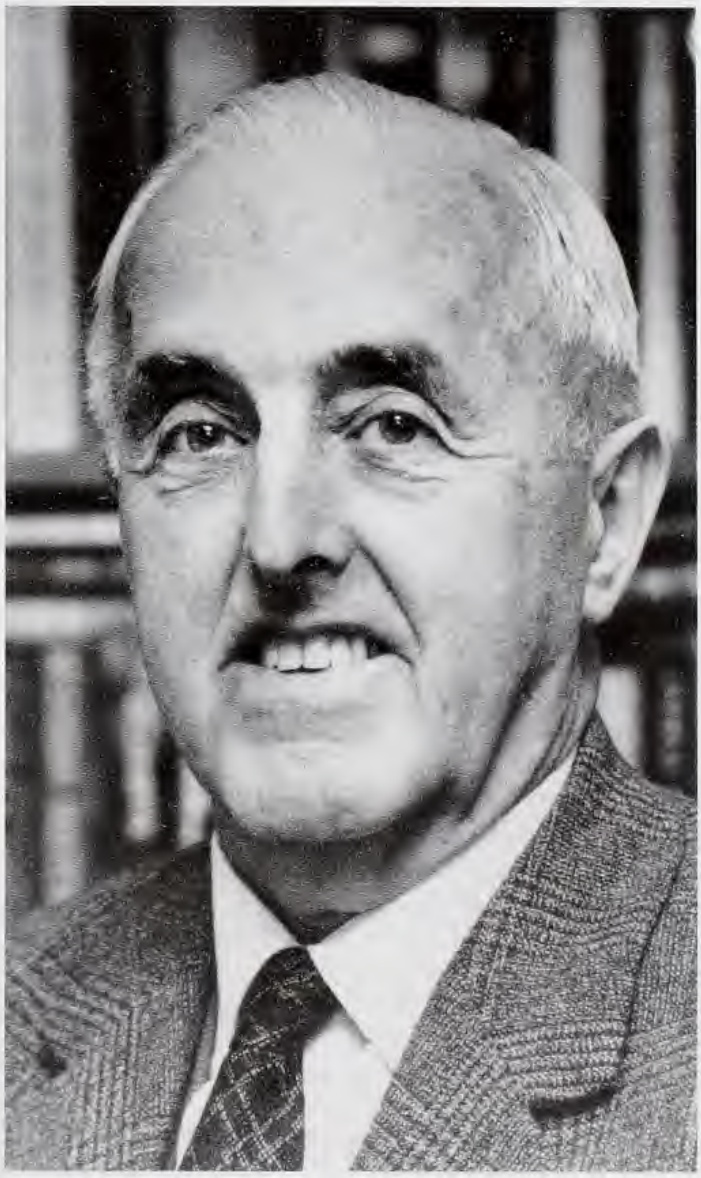


FIG. 1. — Professor Douglas P. WILSON

Source : MNHN, Paris

From an early age DP had been interested in the art of photography and he was a pioneer in the photography of living marine animals on the shore, in tanks, and under the microscope. Indeed, he was almost certainly the first to adapt electronic flash for the photography of living planktonic organisms, his dark-field photomicrographs being particularly impressive, even today. It was for his pioneering work in this field that he received an honorary fellowship of the Royal Photographic Society in 1987.

As well as being remembered by those with a special interest in polychaetes and marine life photography, DP will be remembered by the many hundreds of students who attended the famous easter vacation courses in marine biology at the Plymouth laboratory, for it was he who was the principal organizer of these between 1930 and 1948. Neither will his skills as a popular author be forgotten by those who have copies of "Life of the shore and shallow sea" and "They live in the sea".

Source : MNHN, Paris

## CONTRIBUTED PAPERS

*Cytophysiology, development and reproduction*


**1. Evolution of viviparity in the *genus Ophryotrocha* (Polychaeta, Dorvilleidae)** 29
Bertil ÅKESSON

**2. Environmental influences on endocrine systems controlling reproduction in Polychaetes** 37
Matthew G. BENTLEY, Jeni BOYLE & Allan A. PACLEY

**3. Morphometric analysis of cellular specification in *Platynereis* and *Pomatoceros* embryogenesis (Annelida, Polychaeta)** 45
Adriaan W.C. DORRESTEIJN & Craig Marc LUETJENS

**4. Observations on reproduction and growth of *Sabella spallanzanii* (Polychaeta, Sabellidae) in the Mediterranean Sea** 51
Adriana GIANGRANDE & Angela PETRAROLI

**5. The functional significance plexuses in the ecology of *Ophelia bicornis* Savigny** 57
Tegwyn HARRIS

**6. Feed-back regulation in *Platynereis dumerilii* Audouin & Milne-Edwards, 1833: a status review** 65
Dietrich K. HOFMANN

**7. Bioaccumulation du fer dans le corps cardiaque de *Raricirrus beryli* Petersen & George (Polychaeta, Ctenodrilidae)** 73
Jean VOVELLE, Mary E. PETERSEN, Michèle GRASSET & Patricia BEAUNIER


*Genetics and morphology*


**8. Functional ciliary groups of the feeding palps of Spionid polychaetes** 81
Daniel M. DAUER

**9. Attributes of ribosomal DNA in alvinellid polychaetes from hydrothermal vents** 85
David R. DIXON, Linda R.J. DIXON & Verena TUNNICLIFFE

**10. On the nature of the two anterior asetigerous rings in Dorvilleidae and Dinophilidae (Annelida, Polychaeta)** 93
Danny EIBYE-JACOBSEN

**11. The head of Maldanidae polychaetes of the subfamily Maldanidae** 101
Karen D. GREEN

**12. Effects of sample fixation on body shape of *Capitella capitata* (Polychaeta, Capitellidae)** 111
Maria Nuria MÉNDEZ & Maria José CARDELL

**13. Ultrastructure of sense organs and the central nervous system in *Parenterodrilus taenioides* and their phylogenetic significance in the taxon Protodrilida (Annelida, Polychaeta)** 119
Günter PURSCHKE & Claude JOUIN-TOULMOND

**14. Genome size in Polychaetes: relationship with body length and life habit** 129
R. SOLDI, L. RAMELLA, M. Cristina GAMBI, Paolo SORDINO & Gabriella SELLA


Source : MNHN, Paris

**15. Fine morphology of the feeding apparatus of *Cossura* sp. (Polychaeta, Cossuridae) from the White Sea** 137
Alexander B. TZETLIN

*Phylogeny and taxonomy*

**16. Polychaetes of the family Acoetidae (= Polyodontidae) from the Levant and the Central Mediterranean with a description of a new species of *Eupanthalis*** 145
M. Nechana BEN-ELIAHU & Dieter FIEGE

**17. *Prionospio caspersi* Laubier (Polychaeta, Spionidae) in the Black Sea: long-term monitoring of a population** 163
Temir A. BRITAYEV, Alberto CASTELLI & Tatiana S. AKSIUK

**18. Systematics, ecology and biogeographic relationships in the sub-family Travisiinae (Polychaeta, Opheliidae)** 169
Jean-Claude DAUVIN & Gérard BELLAN

**19. A new species of *Ophryothrocha* (Polychaeta, Dorvilleidae) associated with ice scours in the Canadian Arctic Archipelago** 185
Judith A. FOURNIER & Kathleen E. CONLAN

**20. Two new species of *Branchiomma* (Sabellidae) with redescriptions of closely related species and comments on *Pseudobranchiomma* and *Sabellastarte*** 191
Phyllis KNIGHT-JONES

**21. Redescription of *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830 (Polychaeta, Amphinomidae)** 199
Jerry D. KUDENOV

**22. Sabellariidae (Annelida, Polychaeta) from south America** 209
Paulo da Cunha LANA & Claudia Silvia BREMEC

**23. The phylogenetic position of the Pilargiidae with a cladistic analysis of the taxon - facts and ideas** 223
Frank LICHER & Wilfried WESTHEIDE

**24. *Pseudatherospio fauchaldi* a new genus and species of Spionidae (Polychaeta, Annelida) from the Southern California, USA** 237
Laurence L. LOVELL

**25. *Adercodon pleijeli* gen. and sp. nov. (Polychaeta, Ampharetidae) from the Mediterranean Sea** 241
Andrew S.Y. MACKIE

**26. The genus *Ophryotrocha sensu lato* (Polychaeta, Dorvilleidae) in the Tromsö area, Northern Norway** 251
Eivind OUG

**27. Distributional patterns and taxonomic notes on Lumbrineridae from Crete (S. Aegean, eastern Mediterranean)** 259
K. Nadia PAPADOPOULOU, C. DOUNAS & Chris J. SMITH

**28. Autolytinae (Polychaeta, Syllidae) from Cuba and north American Atlantic Ocean** 269
Guillermo SAN MARTIN

**29. New arctic species of *Scolelepis* (Polychaeta, Spionidae)** 279
Andrew V. SIKORSKI

**30. A systematic problem of inter- and intra-generic variation in nephromixia of Terebellidae** 287
Ralph I. SMITH

**31. Morphometric variation in bifurcate notosetae of two *Euphrosine* species (Polychaete, Euphrosinidae)** 291
Ken D. VOGT & Jerry D. KUDENOV

Source : MNHN, Paris

**32. *Pseudonotomastus southerni* gen. nov., a new capitellid from the Celtic Sea** 299
Lynda M. WARREN & Miles PARKER

**33. A new species of *Chaetozone* (Polychaeta, Cirratulidae) from Europe, with a redescription of *Caulleriella zetlandica* (McIntosh)** 307
Annette WOODHAM & Susan CHAMBERS

**34. Phylogeny of Alciopidae (pelagic polychaetes): a cladistic analysis** 317
Baoling WU & Lua HUA

*Ecology and biogeography*

**35. Preliminary observations on a dense population of *Plyllochaetopterus socialis* Claparède at the sulphurous water boundary in a Mediterranean submarine cave** 323
Marco ABBIATI, L. AIROLDI, Alberto CASTELLI, F. CINELLI & A.J. SOUTHWARD

**36. Contribution of the Polychaetous annelids to the diet of some brazilian fishes** 331
A. Cecília Z. AMARAL, Edmundo F. NONATO & Mônica A.V. PEITI

**37. Ecology of *Pherusa* sp. (Polychaeta, Flabelligeridae)** 339
Analía AMOR

**38. Polychaete fauna associated with the coral *Cladocora caespitosa* (L.) in the eastern Mediterranean** 347
Christos ARVANITIDIS & Athanasios KOUKOURAS

**39. Morphology, ecology, and juvenile development of *Cossura pygodactylata* Jones (Polychaeta, Cossuridae) in Arcachon Bay, SW France, with a reassessment of the geographic distribution of *C. pygodactylata* and *C. soyeri* Laubier** 355
Guy BACHELET & Lucien LAUBIER

**40. Larvae-substrate relationships of *Eupolymnia nebulosa* (Montagu, 1818) (Polychaeta, Terebellidae): an experimental analysis** 371
Michel BHAUD & Jae H. CHA

**41. Is *Owenia fusiformis* a cosmopolitan species?** 383
Jean-Claude DAUVIN & Eric THIÉBAUT

**42. Light influence on larval emission and vertical swimming in the terebellid worm *Eupolymnia nebulosa* (Montagu, 1818)** 405
Jean-Claude DUCHÊNE & Christian NOZAIS

**43. Polychaeta of the German Bight from the 1987 cruise of the R/V "Senckenberg"** 413
Dieter FIEGE & Nechama BEN-ELIAHU

**44. Sélection des grains de sable selon leur nature et leur forme par *Sabellaria alveolata* Linné (Polychète, Sabellariidé) lors de la reconstruction expérimentale de son tube** 425
Yves GRUET & Yves BODEUR

**45. Les vers polychètes et l'estuaire de la Loire au début du 20ème siècle par G. FERRONNIÈRE (1875-1922)** 433
Yves GRUET, Jocelyne MARCHAND & Joseph BAUDET

**46. Temporal and spatial patterns in the distribution of infaunal polychaetes in Jervis Bay, New South Wales, Australia** 441
Patricia HUTCHINGS & C.A. JACOBY

**47. Ecology and biogeochemistry of an *Paralvinella sulfincola* at northeast Pacific hydrothermal vents: review and comparison with *Alvinella* spp. of the east Pacific rise** 453
S. Kim JUNIPER

**48. Polychaete assemblages along a depth gradient in a Spitzbergen Fjord** 463
Michael A. KENDALL

**49. The biogeography of some abyssal polychaetes** 471
Jørgen B. KIRKEGAARD

Source : MNHN, Paris

**50. Preliminary results on recolonization in a small brackish basin on the island of Elba (western Mediterranean)** 479
Claudio LARDICCI & R. BALDI

**51. Intertidal sandy beaches polychaetes of São Sebastião island, Southern Brazil** 485
Eloisa H. MORGADO, A. Cecilia Z. AMARAL, Edmundo F. NONATO & Lara B. SALVADOR

**52. Influence of the tube-building spionid polychaete *Polydora ciliata* on benthic parameters, associated fauna and transport processes** 493
Carola Ilse-Marie NOJI

**53. Patterns of abundance and diversity from the abyss - Polychaetes from northeastern Atlantic abyssal plains** 503
Gordon L.J. PATERSON, John D. GAGE, P. LAMONT, B.J. BETT & M.T. THURSTON

**54. Polychaete response to different aquaculture activities** 511
Patricia POCKLINGTON, David B. SCOTT & C.T. SCHAFER

**55. Influence of temperature and diet on the larval development and growth of juveniles *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae)** 521
Daniela PREVEDELLI

**56. Éthologie alimentaire d'Annélides Polychètes endogées : détermination du niveau sédimentaire où s'effectue la collecte de nourriture** 527
Chantal SALEN-PICARD, Claire GRAHAM & Magali GERINO

**57. Polychaete distribution patterns on *Chlamys patagonica* of the Magellan Strait** 535
Rossana SANFILIPPO

**58. Polychaeta in the estuary of the Piauí River, Sergipe, Brazil** 541
Maria A. SANTOS, C.S.G. SANTOS & C.M.M. OLIVEIRA

**59. Life history of the polychaete *Polydora variegata* that bores into the shells of scallops in Northern Japan** 549
Waka SATO-OKOSHI

**60. Annelid polychaete populations of the Order Eunicida from the southern Gulf of Mexico** 559
Vivianne SOLIS-WEISS, Luz Veronica RODRIGUEZ-VILLANUEVA, Alejandro GRANADAS-BARBA, Victor OCHOA-RIVERA, Luis MIRANDA-VAZQUEZ & Pablo HERNANDEZ-ALCANTARA

**61. Ecological analysis of some Syllidae (Annelida, Polychaeta) from the central Tyrrhenian Sea (Ponza Island)** 567
Alessandra SOMASCHINI & Flavia GRAVINA

**62. Cyclical changes in the fauna associated with tube aggregates of *Ficopomatus enigmaticus* (Fauvel)** 575
Nigel S. THOMAS & Clifford H. THORP

**63. Population variation in *Ficopomatus enigmaticus* (Fauvel) (Polychaeta, Serpulidae) in a brackish water millpond at Emsworth, West Sussex, U.K.** 585
Clifford H. THORP

*Culture and valorisation*

**64. Polychaetes of commercial and applied interest in Italy: an overview** 593
M. Christina GAMBI, Alberto CASTELLI, Adriana GIANGRANDE, Daniela PREVEDELLI & R. ZUNARELLI VANDINI

**65. Polychaeta as a world resource: a review of patterns of exploitation as sea angling baits, and the potential for aquaculture based production** 603
Peter J.W. OLIVE

Source : MNHN, Paris

# Evolution of viviparity in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae)

*Bertil ÅKESSON*

Department of Zoology
University of Göteborg
Medicinaregatan 18
S-413 90 Göteborg, Sweden

ABSTRACT

Brooding is a common feature in the genus *Ophryotrocha*. Viviparity, the most extreme type of parental care, is represented by only one species, *O. vivipara*, but tendencies towards viviparity have also been reported from gonochoric as well as hermaphroditic species. Except for the viviparous species, all species studied deposit their eggs in a gelatinous matrix. The surface of the egg mass may remain soft and sticky, but in two distinct species groups the surface hardens to a solid membrane that encloses gel and eggs. In both groups newly spawned egg masses may occasionally contain a few young larvae. Such larvae never occur in a young female's first egg mass. The larvae are interpreted as originating from fertilized eggs that have been trapped in the coelom of the female during a previous spawning. They develop inside the female at a retarded rate.

In *O. socialis* not only larvae at an early stage of development are released but also larvae/juveniles at more advanced stages. Usually they are released together with a normal spawn, but they may also appear single. Juveniles with up to 12 setigerous segments have been observed. During the normal course of development, the 12-setiger stage is attained after about 80 days. At that age they have already developing oocytes in the coelom whereas the viviparous progeny with the same number of segments have not.

Observations of incipient viviparity in three species groups call for a reevaluation of some previous reports on self-fertilization and on viable larvae obtained in crosses between species that are otherwise reproductively isolated.

RÉSUMÉ

**Évolution de la viviparité dans le genre *Ophryotrocha* (Polychaeta, Dorvilleidae)**

C'est un trait fréquent du genre *Ophryotrocha* d'incuber ses oeufs. La viviparité, le type le plus extrême du soin parental, est représentée chez une espèce, *O. vivipara*, mais des tendances vers la viviparité ont aussi été rapportées chez des espèces gonochoriques aussi bien que chez des espèces hermaphrodites. Exception faite des espèces vivipares, toutes les espèces étudiées déposent leurs oeufs dans une matrice gélatineuse. La surface de la masse d'oeufs peut rester molle et collante, mais dans deux groupes d'espèces distincts, cette surface durcit en une membrane solide qui renferme le gel et les oeufs. Dans les deux groupes, des masses d'oeufs récemment déposées peuvent contenir, de temps en temps, quelques rares larves/juvéniles. De telles larves n'apparaissent jamais dans la première masse d'oeufs d'une jeune femelle. Les larves proviennent probablement d'oeufs fécondés antérieurement qui sont restés dans le coelome de la femelle où ils se sont développés lentement.

Chez *O. socialis* des individus larve/juvénile, à un stade avancé sont relâchés en même temps que des larves en début de développement. Habituellement elles sont émises en même temps qu'une ponte normale, mais elles peuvent aussi apparaître

ÅKESSON, B., 1994. — Evolution of viviparity in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 29-35. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

seules. De tels juvéniles ayant jusqu'à 12 segments sétigères ont été observés. Au cours d'un développement normal ce stade 12 sétigères n'est atteint qu'après environ 80 jours. Ces larves/juvéniles ont alors déjà développé des ovocytes dans le coelome tandis qu'il n'y a pas d'ovocytes dans les juvéniles issus d'un développement vivipare au même stade de développement. Les observations faites sur cette tendance à la viviparité dans les 3 groupes d'espèces nous conduisent à une révision des résultats antérieurs traitant de l'autofécondation et aussi des larves viables qui en réalité n'ont pas été obtenues dans des croisements entre espèces différentes.

## INTRODUCTION

Brood protection has evolved many times among both invertebrates and vertebrates (HOGARTH, 1976; CLUTTON-BROCK, 1991). The same applies also to viviparity, the most extreme form of brood protection. Evidence from most groups indicates that viviparity has evolved from oviparous ancestors and that internal fertilization has been a preadaptation for the evolution of viviparity. In transition stages fertilized eggs have been retained for progressively longer periods of time. They do not receive any nutrients from the female and this holds true also for species with ovoviviparity, the least advanced form of viviparity. In more advanced viviparous forms, the female continues to provide the embryos with nutrients. Often a kind of placenta analogue develops or the embryo/larva receives nutrients from surrounding body fluids of the female.

For the evolution of viviparity from oviparous ancestors to occur, transition stages must also be selected. The continuing discussion has been widened to involve other aspects of brood protection and its relation to egg size. SHINE (1978) suggested the "safe harbor" hypothesis according to which optimal offspring size is determined by relative mortality rates of egg stages and free-living juveniles. Selective forces tend to maximize the time spent in the safest stages of development. In brooders eggs are safer than juveniles which should account for the positive correlation often seen between brood protection and large egg size (SHINE, 1989; CLUTTON-BROCK, 1991).

According to HOGARTH (1976), evolution towards viviparity is favoured in species that already produce a restricted number of eggs. Retention and viviparity protect the progeny against both predators and harsh environmental conditions such as cold climate, desiccation or, for marine animals, suboptimal salinity levels.

Viviparity has been reported from several polychaete families and SCHROEDER & HERMANS (1975) have listed 19 species. However, for 9 of these the original reports on viviparity have not been verified in later studies. Many older reports on viviparity were analyzed by SMITH (1950) who provided evidence that some of them were erroneous. Some embryos or larvae from inside the body of polychaetes were either developmental stages of parasitic polychaetes or turbellarians.

The purpose of this paper is to describe a possible line of evolution towards viviparity in the genus *Ophryotrocha* of the family Dorvilleidae. Dorvilleid polychaetes are generally small and many of the smallest, nonparasitic species belong to the genus *Ophryotrocha*. Only three species exceed a length of 10 mm. Two of these are commensals in the gill chamber of crabs (MARTIN *et al.*, 1991), the third one is found near geothermal vents (BLAKE, 1985). The smallest of all *Ophryotrocha* species, *O. vivipara* Banse, 1963, is only 0.8-1 mm long. BANSE's description was based on two specimens from the vicinity of Friday Harbor, Washington. This was the only record until I collected about 50 specimens in the aquarium of the Tjärnö marinbiologiska laboratorium located about 200 km north of Gothenburg. *Ophryotrocha vivipara* is one of the few species that I have failed to maintain as a laboratory culture; nontheless BANSE's observation of a truly viviparous species could be confirmed. The juveniles have two or three setigerous segments when released from the posterior end of the female.In contrast to a uniform adult morphology in most species, reproduction is remarkably variable. In addition to the traits listed in Table 1, species or species groups may also vary in other reproductive adaptations such as clutch size and time between consecutive spawnings, sex ratio in gonochoric species and amount of energy allocated to individual eggs (ÅKESSON, 1973).

Mating behaviour is equally variable. SELLA (1985, 1988) analyzed pair formation and egg trading in the simultaneous hermaphrodite *O. diadema*. A behaviour has evolved that safeguards against non-reciprocating partners. In gonochoric species, females often discriminate against males from other geographic populations and they certainly do so in interspecific crosses (ÅKESSON, 1972a, 1977b, 1978, 1984). In the protandrous hermaphrodite *O. puerilis*, sex reversal may occur several times in the same individual. In pair cultures with females, the result of fights over sex will be that the winner remains female and the loser changes to male. BERGLUND (1991) has shown that females prefer small mal es. If a female mates with a large male, she is at risk of being challenged to change sex when she is weakened after spawning.

Source : MNHN, Paris

TABLE 1. — Reproductive traits in the genus *Ophryotrocha*.

| | KEY REFERENCES |
|---|---|
| Germ cells are not shed freely into the water. Pseudocopulation ensures fertilization | REMANE, 1952; SWEDMARK, 1964 |
| No pelagic larvae (but demersal, lecitotrophic larvae in *O. maculata*) | ÅKESSON, 1973 |
| Short generation length | |
| Semicontinuous reproduction | ÅKESSON, 1982, 1984 |
| Gonochoric species: (A) with sexual di morphism, (B) with 'inducible hermaphroditism', (C) with facultative hermaphroditism and self fertilization, (D) with environmental sex determination | (A) ÅKESSON, 1972b; ZAVARZINA & TZETLIN, 1986, 1991; OUG, 1990. (B) BACCI *et al.*, 1979, (C) PARENTI, 1960; ÅKESSON, 1984. (D) ROLANDO, 1982, 1984; SELLA & RAMELLA, pers. com. |
| Uneven allocation to male and female function in simultaneous hermaphrodites | SELLA, 1990; OCKELMANN & ÅKESSON, 1989 |
| Egg trading | SELLA, 1985, 1988 |
| Both sequential and simultaneous hermaphrodites; in one species age (size)-related change from hermaphrodite to female | ÅKESSON, 1984; PARENTI, 1964 |
| Cross fertilization the rule, but selfing possible in some hermaphrodites | PARENTI, 1960; ÅKESSON, 1984; OCKELMANN & ÅKESSON, 1989 |
| Brooding of (A) large gelatinous egg masses with sticky surface, (B) egg masses with hard surface, (C) egg masses deposited in tubes made by the parents | ÅKESSON, 1984; OUG, 1990 |
| Incipient viviparity in two species groups, viviparity in one species | BANSE, 1963; this paper |

Incipient viviparity has been reported from the simultaneous hermaphrodite *O. diadema* (ÅKESSON, 1973, 1976). Occasionally one or two larvae appear in newly spawned egg masses, but never in a female's first brood. The fusiform egg masses of *O. diadema* are surrounded by a tough wall and larvae cannot enter an egg mass from the outside.

As in all other known *Ophryotrocha* species, fertilization in *O. diadema* is preceded by a kind of pseudocopulation similar to that described by Westheide from O. gracilis (WESTHEIDE, 1984, fig. 3). Selfing has not been observed. Eggs and spermatozoa are shed into a gelatinous matrix and mingle there. The egg mass is molded to its final shape and usually attached to a substratum. Then the surface of the mucus hardens to form the tough outer wall.

The explanation suggested for the presence of larvae in newly spawned egg masses is that a few eggs have been trapped in the female part of the coelom during a previous spawning. They have been fertilized by entering spermatozoa, developed inside the body, and then released together with the next spawn (ÅKESSON, 1976).

The same type of incipient viviparity as in O. diadema has also been observed in several members of the labronica group, a group of related gonochoric species within the genus (ÅKESSON, 1973). Members of that group produce a different kind of egg mass that is tube-shaped and contains smaller, but more numerous eggs than that of *O. diadema*. Enclosed larvae inside newly spawned egg masses have been observed in *O. labronica*, *O. notoglandulata*, and *O. macrovifera*, and they may occur in all members of the labronica group.

*Ophryotrocha socialis*, another simultaneous hermaphrodite, was recently described by OCKELMANN & ÅKESSON (1989). The gelatinous matrix around the eggs is sparse in this species but there is enough to attach the eggs to each other forming tubular or irregular egg masses. As in *O. diadema* fertilization takes place after pseudocopulation. Isolated individuals may self-fertilize but such self-fertilization is external.

In a still ongoing life table study that began with fertilized eggs, 0-setiger larvae occasionally appeared in the bowls when the experiment had continued for about 6 months. The larvae were at the stage of development that is normally obtained in 3 weeks (OCKELMANN & ÅKESSON,1989, Fig.10). Since the adult worms were transferred to clean bowls once a week, these larvae could not be the result of a previous spawn. Eventually more advanced larvae could also be collected, i.e., larvae with 1-2 or more setigerous segments. The peak production of such larvae was observed when the adults were 10 months old and had 19-20 setigerous segments. In one week 40 adults had produced 11 0-setiger larvae

Source : MNHN, Paris

and 17 juveniles with 7-12 setigers (mean 9.9 ± 0.4). In addition, the adults had spawned 919 eggs during the same week.

After a normal spawning, the progeny develops into functional males with 6 setigers after about 50 days. The first spawning was observed at an age of 60 days in worms with 10 setigers. Only few worms spawn before the 11-setiger stage (OCKELMANN & ÅKESSON, 1989). Not even the largest viviparous progeny had any visible oocytes in the coelom. They were more slender than larvae with the same number of setigers that develop after normal spawning. It has not been possible to determine the age of the viviparous progeny when released from the coelom.

## REEVALUATION OF SOME PREVIOUS REPORTS

The observations of incipient viviparity in two species groups as well as mixed oviparity and viviparity in *O. socialis* may justify a reevaluation of some previous reports on self-fertilization and on results of crossing experiments.

HARTMANN (1943) and BACCI (1978) reported on rare instances of self-fertilization in *O. puerilis*. In some crosses between the Atlantic and Mediterranean subspecies of *O. puerilis*, a very low percentage of spawned eggs were reported to develop into viable larvae (ÅKESSON, 1973). The possibility should be considered that these reports concern incipient viviparity of the same kind as in *O. diadema* and the labronica group. However, it is evident that some species may reproduce by both cross-fertilization and self-fertilization. This is true of *O. labronica* ( but note the discussion about identity of species in ÅKESSON, 1984), *O. socialis*, and a not yet described species from Florida (LA GRECA & BACCI, 1962; PARENTI, 1960; ZUNARELLI, 1962; ZUNARELLI-VANDINI, 1967; ÅKESSON, 1984; OCKELMANN & ÅKESSON, 1989).

In the light of these findings, the previous report on partial success in crosses between the Pacific species *O. notoglandulata* and *O. labronica pacifica* should be reevaluated. ÅKESSON (1984) reported that occasionally a few (< 10) viable hybrids were obtained in crosses between female *O. notoglandulata* and male *O. l. pacifica*. These supposed hybrids were all female and therefore $F_2$ hybrid breakdown could not be tested. No progeny was obtained in backcross with *O. l. labronica* males except for a few larvae. As in the first cross, the number of larvae per egg mass was always below 10. In backcross with *O. notoglandulata* many egg masses were produced, usually with almost 100 % development.

A return to the original data sheets revealed that in the interspecific cross only 5 "hybrids" developed into normal, mature females. They were first used in backcross with male *O. notoglandulata* and then with *O. l. labronica*. Previous and subsequent crosses between *O. labronica* (both subspecies) and *O. notoglandulata* proved to be intersterile. More than 100 egg masses in each reciprocal cross have been observed. Moreover, the "hybrid" progeny reported by ÅKESSON (1984) was all female. The same was true of all viviparous progeny observed so far in the three gonochoric species where incipient viviparity has been recorded. A very likely explanation of the crossing results (ÅKESSON, 1984) is that the few larvae obtained were an expression of incipient viviparity.

In recent experiments with both inter- and intraspecific crosses, individual egg masses have been analyzed for enclosed larvae. Such larvae are found in less than 5 % of the egg masses and only in egg masses produced by females that have spawned previously. The fact that such larvae were produced in two subsequent generations in the crosses reported by ÅKESSON (1984) may indicate a heritability of the trait, but recent selection experiments with viviparous progeny has not yet proved this.

## DISCUSSION

For the evolution of viviparity in the genus *Ophryotrocha*, transition stages between oviparity and viviparity should have a selective advantage. One such advantage may be that those embryos that are retained in the female's body have better chances of survival than the siblings which are fertilized and spawned at the same time. A brooding worm presumably has better chance of escaping a predator than embryos enclosed in an immobile egg mass that the female will desert when attacked.

Internal fertilization as a prerequisite for viviparity is not fulfilled in *Ophryotrocha*, but functionally the kind of pseudocopulation found in the genus comes close to internal fertilization (WESTHEIDE, 1984). The final stage, obligate viviparity, is found in the smallest known *Ophryotrocha* species only. This may be an indication that the evolution of viviparity is one of many adaptations to 'the problem of being small'. As has been repeatedly discussed for meiofauna species (SWEDMARK, 1964; WESTHEIDE, 1984), smaller size is correlated with changes in

Source : MNHN, Paris

reproductive traits compared to related larger species. WESTHEIDE (1987) demonstrated how progenetic (neotenic) evolution has been one of the major forces behind adaptation to the interstitial habitat. The morphology of an adult *Ophryotrocha* is very similar to the larval morphology of larger eunicid polychaetes, e.g., to the larvae of *Dorvillea rudolphi* (RICHARDS, 1967). The evolution of progenesis is also demonstrated in WESTHEIDE's (1987) series of increasingly juvenile characters in dorvilleid genera where the endpoint is the dinophilid genus *Dinophilus*. It has been shown that dinophilids are closely related to eunicids (HERMANS, 1969; ÅKESSON, 1977a; WESTHEIDE, 1985).

Reproduction in the genus *Ophryotrocha* is more variable than in any other polychaete taxon of similar size. Energetic constraints related to small size may be one reason; opportunistic life histories with often sparse populations may be another. The most important of those reproductive traits are listed in Table 1.

WESTHEIDE's (1987) series of successive embryonization in the family Dorvilleidae indicates that small species have evolved from larger ones. ---"these small interstitial species must then form the end-point of an evolutionary line which originates in larger benthic species" (WESTHEIDE, 1984, p 266). For the genus *Ophryotrocha* it has also been suggested that the atrochal, demersal larvae found in *O. maculata* occurred in the larger ancestors (ZAVARZINA & TZETLIN, 1991). Obviously the progenetic evolution has been very successful and has triggered an adaptive radiation.

The egg diameter varies between 240-320 µm in *O. cosmetandra* (OUG, 1990) and 56.5 µm in *O. paralabidon* (HILBIG & BLAKE, 1991). At the end of the brooding period, the progeny of some species is released as polytrochous larvae with no setigerous segments, whereas other species release juveniles with up to 5 setigers. In *O. vivipara* the progeny has only 2-3 setigers when released, but the largest recorded viviparous progeny of *O. socialis* had 12 setigers.

In summary, the variability in reproductive traits in the genus *Ophryotrocha* makes it an extremely valuable study material, a kind of marine *Drosophila*. "This genus may be very important for sex allocation studies, since it contains all three of the basic forms of sexuality found in animals" (CHARNOV, 1982, p 201).

## REFERENCES

ÅKESSON, B., 1972a. — Incipient reproductive isolation between geographic populations of *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Zool. Scr.*, **1** : 207-210.

ÅKESSON, B., 1972b. — Sex determination in *Ophryotrocha labronica* (Polychaeta, Dorvilleida). *In*: B. BATTAGLIA (ed), *Fifth European Marine Biology Symposium*. Piccin Editore, Padova : 163-172.

ÅKESSON, B.,1973. — Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). *Zool. Scr.*, **2** : 145-155.

ÅKESSON, B.,1976. — Morphology and life cycle of *Ophryotrocha diadema*, a new polychaete species from California. *Ophelia*, **15** : 23-35.

ÅKESSON, B., 1977a. — Parasite-host relationships and phylogenetic systematics. The taxonomic position of Dinophilids. *Mikrofauna Meeresboden*, **61** : 19-28.

ÅKESSON, B., 1977b. — Crossbreeding and geographic races: Experiments with the polychaete genus *Ophryotrocha*. *Mikrofauna Meeresboden*, **61** : 11-18.

ÅKESSON, B.,1978. — A new *Ophryotrocha* species of the *labronica* group (Polychaeta, Dorvilleidae) revealed in cross-breeding experiments. *In*: B. BATTAGLIA & J.A. BEARDMORE (eds), *Marine Organisms. Genetics, Ecology and Evolution*. Plenum Press, New York and London : 573-590.

ÅKESSON, B., 1982. — A life table study on three genetic strains of *Ophryotrocha diadema* (Polychaeta, Dorvilleidae). *Internat. J. Invertebr. Reprod.*, **5** : 59-69.

ÅKESSON, B.,1984. — Speciation in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *In*: A. FISHER & H.-D. PFANNENSTIEL (eds), Polychaete Reproduction. Progress in Comparative Reproductive Biology. *Fortschr. Zool.*, **29** : 299-316.

BACCI, G., 1978. — Genetics of sex determination in *Ophryotrocha* (Annelida, Polychaeta). *In*: B. BATTAGLIA & J.A. BEARDMORE (eds), *Marine Organisms. Genetics, Ecology and Evolution*. Plenum Press, New York and London : 549-571.

BACCI, G., LANFRANCO, M., MANTELLO, I. & TOMBA, M., 1979. — A new pattern of hermaphroditism (inducible hermaphroditism) in populations of *Ophryotrocha labronica* (Annelida, Polychaeta). *Experientia*, **35** : 605-606.

Source : MNHN, Paris

BANSE, K., 1963. — Polychaetous Annelids from Puget Sound and the San Juan Archipelago, Washington. *Proc. biol. Soc. Wash.*, **76** : 197-208.

BERGLUND, A., 1991. — To change or not to change sex: a comparison between two *Ophryotrocha* species (Polychaeta). *Evol. Ecol.*, **5** : 128-135.

BLAKE, J.A.,1985. — Polychaeta from the vicinity of deep-sea geothermal vents in the Eastern Pacific. I. Euphrosinidae, Phyllodocidae, Hesionidae, Nereidae, Glyceridae, Dorvilleidae, Orbiniidae, and Maldanidae. *Biol. Soc. Wash. Bull.*, **6** : 67-101.

CHARNOV, E.L., 1982. — *The theory of sex allocation*. Princeton Univ. Press, Princeton, New Jersey, 355 pp.

CLUTTON-BROCK, T.H., 1991. — *The Evolution of Parental Care*. Princeton Univ. Press, Princeton, New Jersey, 352 pp.

HARTMANN, M., 1943. — *Die Sexualität*. Gustav Fischer, Jena, 393 pp.

HERMANS, C.O., 1969. — The systematic position of the Archiannelida. *Syst. Zool.*, **18** : 85-102.

HILLBIG, B. & BLAKE, J.A., 1991. — Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with a generic revision of *Ophryotrocha*. *Zool. Scr.*, **29** : 147-183.

HOGARTH, P.J., 1976. — *Viviparity*. Edvard Arnold, London, 69 pp.

LA GRECA, M. & BACCI, G., 1962. — Una nuova specie di *Ophryotrocha* delle coste tirreniche. *Boll. Zool.*, **29** : 13-23.

MARTIN, D., ABELLO, P. & CARTES, J., 1991. — A new species of *Ophryotrocha* (Polychaeta: Dorvilleidae) commensal in *Geryon longipes* (Crustacea: Brachyura) from the Western Mediterranean Sea. *J. nat. Hist.*, **25** : 279-292.

OCKELMANN, K.W. & ÅKESSON, B., 1989. — *Ophryotrocha socialis* n.sp., a link between two groups of simultaneous hermaphrodites within the genus (Polychaeta, Dorvilleidae). *Ophelia*, **31** : 145-162.

OUG, E., 1990. — Morphology, reproduction, and development of a new species of *Ophryotrocha* (Polychaeta, Dorvilleidae) with strong sexual dimorphism. *Sarsia*, **75** : 191-201.

PARENTI, U., 1960. — Self-fertilization in *Ophryotrocha labronica*. *Experientia*, **16** : 413-414.

PARENTI, U., 1964. — Inversione sessuale limitata a due metameri in *Ophryotrocha gracilis*. *Boll. Zool.*, **31** : 25-31.

REMANE, A., 1952. — Die Besiedlung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. *Verh. dt. zool. Ges.*, **1951** : 327-359.

RICHARDS, T.L., 1967. — Reproduction and development of the polychaete *Stauronereis rudolphi*, including a summary of development in the superfamily Eunicea. *Mar. Biol.*, **1** : 124-133.

ROLANDO, A., 1982. — Sexual conditions in a population of *Ophryotrocha robusta* (Annelida, Polychaeta) from Genoa. *Memorie Soc. tosc. Sci. nat.* (B), **89** : 145-152.

ROLANDO, A., 1984. — The sex induction hypothesis and reproductive behaviour in four gonochoristic species of the genus *Ophryotrocha* (Annelida, Polychaeta). *Monit. zool. ital.*, (N.S.), **18** : 287-299.

SCHROEDER, P.C. & HERMANS, C.O., 1975. — Annelida; Polychaeta. *In*: A.C. GIESE & J.S. PEARSE (eds), *Reproduction of Marine Invertebrates. Vol. III: Annelids and Echiurans*. Academic Press, New York, San Francisco, London : 1-213.

SELLA, G., 1985. — Reciprocal egg trading and brood care in a hermaphroditic polychaete worm. *Anim. Behav.*, **33** : 938-944.

SELLA, G., 1988. — Reciprocation, reproductive success and safeguards against cheating in the mating system of a hermaphroditic polychaete worm. *Biol. Bull.* (Woods Hole), **175** : 212-217.

SELLA, G., 1990. — Sex allocation in the simultaneously hermaphroditic polychaete worm *Ophryotrocha diadema*. *Ecology*, **71** : 27-32.

SHINE, R., 1978. — Propagule size and parental care. The "safe harbor" hypothesis. *J. theoret. Biol.*, **75** : 417-424.

SHINE, R., 1989. — Alternative models for the evolution of offspring size. *Am. Nat.*, **134** : 311-317.

SMITH, R.I., 1950. — Embryonic development in the viviparous nereid polychaete, *Neanthes lighti* Hartman. *J. Morphol.*, **87** : 417-466.

SWEDMARK, B., 1964. — The interstitial fauna of marine sand. *Biol. Rev.*, **39** : 1-42.

Source : MNHN, Paris

WESTHEIDE, W., 1984. — The concept of reproduction in polychaetes with small body size: adaptations in interstitial species. *In*: A. FISCHER & H.-D. PFANNENSTIEL (eds), Polychaete Reproduction. Progress in Comparative Reproductive Biology. *Fortschr. Zool.*, **29** : 265-287.

WESTHEIDE, W., 1985. — The systematic position of the Dinophilidae and the archiannelid problem. *In*: S. CONWAY MORRIS Morris, D. GEORGE, R. RIBSON & H.M. PLATT (eds), *The Origin and Relationships of Lower Invertebrates*. Oxford Univ. Press, Oxford : 310-326.

WESTHEIDE, W., 1987. — Progenesis as a principle in meiofauna evolution. *J. nat. Hist.*, **21** : 843-854.

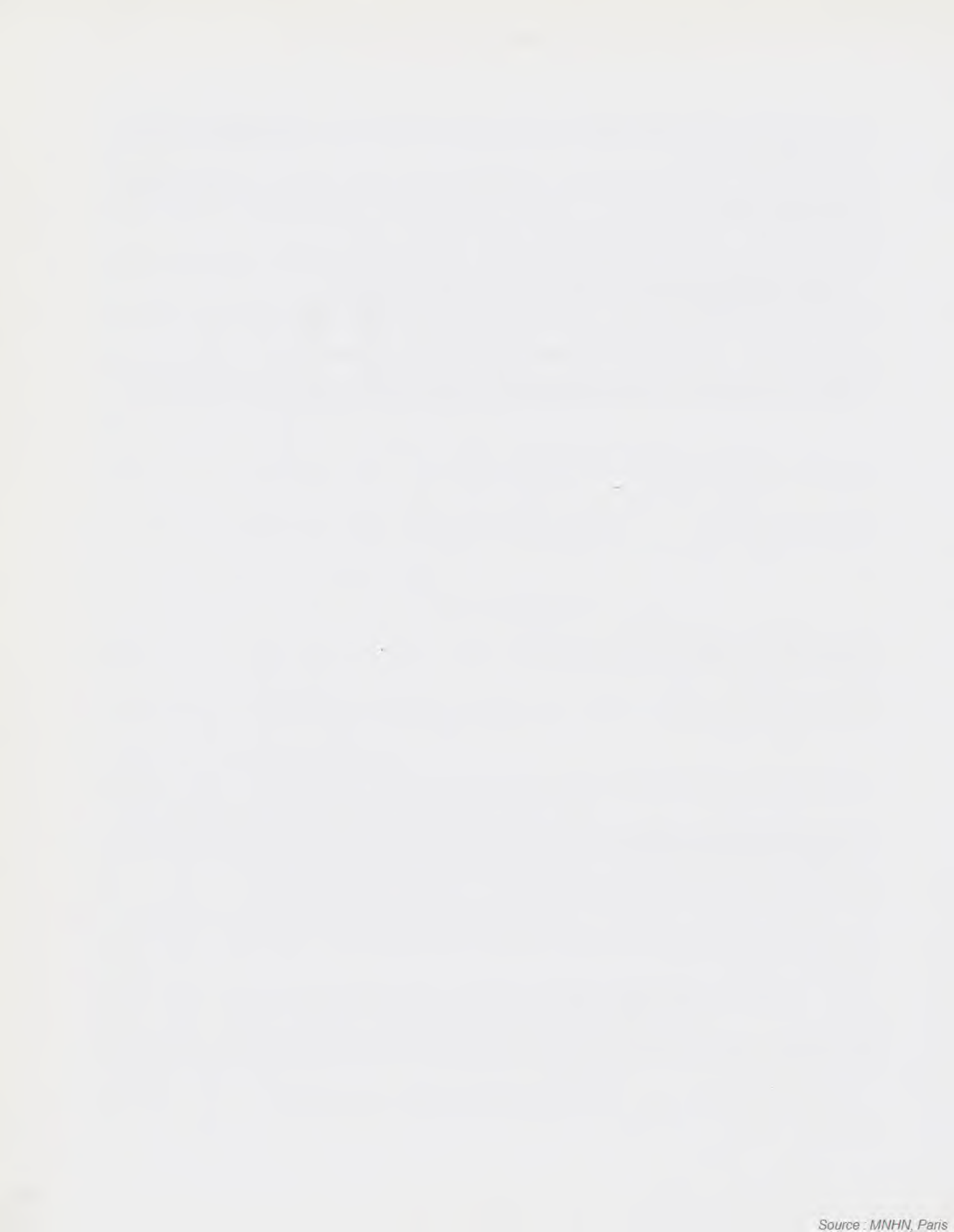
ZAVARZINA, E.G. & TZETLIN, A.B., 1986. — Biology of *Ophryotrocha dimorphica* sp.n. (Polychaeta, Eunicida) from Peter the Great Bay (the Japan Sea). *Zool. Zh.*, **65** : 1808-1817. (In Russian, English summary).

ZAVARZINA, E.G. & TZETLIN, A.B., 1991. — Breeding and larval morphology of *Ophryotrocha dimorphic*a Zavarzina & Tzetlin (Polychaeta: Dorvilleidae). *Ophelia*, Suppl., **5** : 411-420.

ZUNARELLI, R., 1962. — Il differenziamento citosessuale di tre specie di *Ophryotrocha*. *Boll. Zool.*, **29** : 417-423.

ZUNARELLI-VANDINI, R., 1967. — Azioni reciproche sulle gonadi in coppie omeospecifiche ed eterospecifiche di *Ophryotrocha puerilis siberti* ed *Ophryotrocha labronica*. *Arch. Zool. Ital.*, **52** : 179-192.

Source : MNHN, Paris



Source : MNHN, Paris

# Environmental influences on endocrine systems controlling reproduction in Polychaetes

*Matthew G. BENTLEY, Jeni BOYLE * & Allan A. PACEY***

Gatty Marine Laboratory, School of Biological and Medical Sciences
University of St Andrews, St Andrews KY16 8LB, Scotland, U.K.
*present address: Clyde River Purification Board, East Kilbride
Glasgow G75 0LA, Scotland, U.K.
**present address: Observatoire Océanologique, URA CNRS 671
B.P.28, 06230 Villefranche-sur-Mer, France

## ABSTRACT

Photoperiod and/or temperature are known to influence gametogenesis and spawning in a number of polychaete species. Information is now available on the nature of endocrine systems controlling gametogenesis and spawning in representatives of several polychaete families. For relatively few species, however, is information available on the possible transduction of environmental signals by the endocrine system (BENTLEY & PACEY, 1992). We report here on the effects of photoperiod and temperature on the action of gonadotropin and spawning hormones in the polychaete *Nephtys hombergii*, and on the action of a gonadotropin hormone in the polynoid *Harmothoe imbricata*.

## RÉSUMÉ

**Influences des facteurs externes sur les systèmes endocrines contrôlant la reproduction chez les Polychètes**

La photopériode et/ou la température agissent sur les processus de gamétogenèse et de ponte chez un grand nombre d'espèces de polychètes. Si les différents types de systèmes endocrines qui contrôlent la gamétogénèse et la ponte sont bien documentés chez de nombreuses espèces de polychètes, on a, par contre, très peu d'informations sur les interactions existant entre les facteurs du milieu et ces systèmes endocrines (BENTLEY & PACEY, 1992). Nous rapportons ici les effets de la photopériode et la température sur l'action de l'hormone gonadotropique et de l'hormone de ponte chez *Nephtys hombergii* ainsi que sur l'action de l'hormone gonadotropique, qui a récemment été décrite, chez *Harmothoe imbricata*.

## INTRODUCTION

*Nephtys hombergii* Savigny, 1818 (Nephtyidae) and *Harmothoe imbricata* L., 1769 (Polynoidae) are both iteroparous polychaetes with an annual cycle of reproduction. *Nephtys hombergii* produces a single batch of gametes which are spawned in late April or May in populations around the coast of northern England or Scotland (OLIVE, 1978; BENTLEY *et al.*, 1984). *Harmothoe imbricata*, in contrast, produces two consecutive batches of gametes which are produced and spawned in quick succession in the spring (DALY, 1972, 1974; GARWOOD,

BENTLEY, M.G., BOYLE, J. & A.A. PACEY, 1994. — Environmental influences on endocrine systems controlling reproduction in Polychaetes. *In:* J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 37-44. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

1981). Gametogenesis and spawning in *N. hombergii* are controlled by two hormones, a gonadotropin hormone and a spawning hormone (OLIVE, 1976; OLIVE & BENTLEY, 1980; BENTLEY & OLIVE, 1982; OLIVE & LAWRENCE, 1990) but to date, evidence for the influence of any environmental factors on reproduction has been speculative. A possible correlation was reported, for example, between insolation and daytime spawning of *Nephtys caeca* (BENTLEY *et al.*, 1984).

Studies on *Harmothoe imbricata* have revealed a sophisticated photoperiodic control of reproduction (GARWOOD & OLIVE, 1978, 1982; CLARK, 1988) but, only recently has a gonadotropin hormone been shown to operate in the control of oogenesis (OLIVE *et al.*, 1990). The first cohort of oocytes requires appropriate environmental input and endocrine support. The second oocyte cohort has been shown to develop autonomously, apparently without environmental control.

The results we describe in this paper show that in *Nephtys hombergii* environmental conditions under which animals are maintained may affect resorption and the onset of renewed gametogenesis. Resorption has been shown to be a common occurrence following spawning failure in this species (OLIVE *et al.*, 1981). We also show that there is endocrine support of development of the second cohort of oocytes in *Harmothoe imbricata* even though these do not require continued environmental support. In light of the fact that rapid growth of the first cohort of oocytes occurs under gonadotropin support apparently associated with increasing photoperiod in the spring (CLARK, 1988) then observations that continued gonadotropin secretion occurs, without further environmental stimulus, during the rapid vitellogenesis of the second oocyte cohort are as would be predicted.

## MATERIALS AND METHODS

Collection and maintenance of specimens. — Specimens of *Nephtys hombergii* were collected by digging in sand at low water of spring tides from three sites: 'The Black Middens' in the estuary of the River Tyne, North-East England; Kirkcolm, Wigtownshire, Scotland and from Fairlie Sands, Ayrshire, Scotland. Individuals were maintained in the laboratory in groups of four in polyethylene containers containing 200ml sea water and sterilised sand to a depth of 1cm.

Specimens of *Harmothoe imbricata* were collected from beneath stones from the intertidal rocky shore at St. Andrews and Kingsbarns, Fife, Scotland. They were maintained individually in small glass jars containing 50ml of seawater. An empty *Patella vulgata* shell was included to provide shelter. Animals which were not used within one week of collection were fed weekly with pieces of *Nereis diversicolor* presented in forceps.

Light temperature regimes for laboratory maintenance of animals. — Animals were maintained in the laboratory in Gallenkamp cooled incubators with timed light cycling under a variety of environmental conditions as appropriate. The particular combinations of photoperiod and temperature were as follows:

Ambient conditions

Summer conditions of daylength and temperature 16L: 8D, 15°C

Winter conditions of daylength and temperature 8L: 16D, 5°C

Winter daylength / summer temperature 8L: 16D, 15°C

Continuous illumination, 7°C.

Sampling of coelomic / ovarian oocytes. — *Nephtys hombergii* were anaesthetized in 0.07% 3-aminobenzoic acid ethyl ester (Sigma Chemical Co.) in sea water. Samples of coelomic / ovarian oocytes were obtained by puncturing the body wall in the inter-parapodial region with a pulled micro-pipette which had been moistened with filtered sea water. Examination was carried out on a Leitz Diaplan compound microscope using a x40 objective lens.

Extraction of brain homogenates and their preparation for use in tissue culture. — Supra-oesophageal ganglia ("brains") were removed from *Nephtys hombergii* anaesthetized as described above by making a transverse incision in the dorsal body wall just posterior to the prostomium. Excised ganglia were kept on ice until homogenization. Homogenization was carried out using an MSE Soniprep 150 ultrasonic disintegrator fitted with a 9mm titanium steel probe. Crude extracts to be used for immediate bioassay or to be lyophilised for storage were homogenised in bidistilled water, the aqueous supernatant was then used for injection or lyophilised and stored at -20°C until used. Heat treated homogenate was prepared by suspending tubes containing crude homogenate in a water bath at 100°C for 1 min followed by centrifugation in an MSE micro-centaur; the supernatant was then used for subsequent addition to tissue culture wells.

Bioassay procedures for SH in *Nephtys*. — The bioassay of extracts of supra-oesophageal ganglia for Spawning Hormone (SH) activity was carried out as follows: gravid specimens of *Nephtys hombergii* were

Source : MNHN, Paris

anaesthetized as above and injected with extract to be assayed or with filtered sea water as a control. Injections of 10µl volume were made with a pulled, calibrated glass micropipette. The animals were then placed in an incubator at 12°C and allowed to recover from the anaesthetic. The spawning response was measured using standard counts of spawned gametes as described previously (OLIVE & BENTLEY, 1980).

Aseptic techniques. — *Culture method.* Animals were placed in streptomycin (2.5 mg/ml) and penicillin (5000IU/ml) for a period of 24 h before dissection of ovaries for tissue culture. Animals were anaesthetized as described above and ovaries were removed by excision of parapodia and lifting out of the ovaries with sterile watchmaker's forceps. The ovaries from several females were pooled for use in amino-acid incorporation experiments, where they were explanted into culture wells of Cel-Cult 24-well plastic tissue culture plates (Sterilin) each containing 2 ml of culture medium developed by BENTLEY & OLIVE (1982) for polychaete organ culture.

Radio-isotope procedures. — Ten ovaries were added to each tissue culture well. L-[4,5-$H^3$] leucine (Amersham International; specific activity 130-190 $Ci.mM^{-1}$) (≈10,000 $counts.well^{-1}$) ). The plates were placed in sealed containers with moist tissue and kept in Gallenkamp cooled incubators at 15°C.

*Harvesting of Cultures.* — After culture periods of 96 h the ovaries and medium were removed from the wells and centrifuged briefly in an MSE micro-centaur to sediment the ovaries. The medium was discarded, the ovaries were resuspended in 1ml of 0.125 M Tris-HCl buffer at pH 8.5 and then homogenised in a Potter glass homogeniser. An aliquot of 0.5 ml (50%) of the homogenate was stored for subsequent protein analysis using the Bradford micro-protein determination method (BRADFORD, 1976). Three ml of ice-cold TCA was added to the remaining 0.5 ml of homogenate and this was left overnight at 4°C. The samples were centrifuged (at 2800g) in a MSE Mistral 3000 centrifuge for 30 min at 4°C. The supernatant was removed and 1ml of 0.15M NaOH was added to redissolve the proteins. The sample was divided into two, 3 ml Packard emulsifier scintillant 299 was added and the sample was then counted for 10 min on a Packard 2000 Tri-Carb liquid scintillation analyzer.

## RESULTS

Observations on *Nephtys* gametogenesis. — Means and ranges of oocyte sizes in individuals which had been maintained under conditions of: a) winter photoperiod (8L: 16D) and temperature (5°C); c) summer photoperiod (16L:8D) and temperature (15°C); d) continuous illumination at 7°C; or b) recently collected from the field in September 1990 are represented in Fig. 1. It can be seen that group a) which had been maintained under winter conditions six of the 19 individuals had no vitellogenic eggs (diameter > 50 µm ) and the mean oocyte diameter was <80 µm in eight of them. In contrast large vitellogenic eggs were found in virtually all worms in the other three groups. These observations were made on individuals taken from a field population which did not spawn in 1990 and which at the commencement of the experiment had unspawned vitellogenic oocytes in the coelom. It is quite clear that resorption of unspawned oocytes is accelerated in individuals maintained under conditions of winter temperature and photoperiod. Maintenance under low temperature alone (d) does not have the same effect.

Observations on *Nephtys* spawning hormone activity. — The results of assay of spawning-inducing activity of *Nephtys hombergii* supra-oesophageal ganglia taken from individuals which had been maintained under a range of photoperiod/ temperature regimes for a period of 219 days (from prior to the winter solstice) are shown in Fig. 2. Individuals injected with supra-oesophageal ganglion homogenate prepared from freshly collected animals show a response typical of *Nephtys hombergii*, both in terms of the numbers of gametes released and the percentage of individuals responding. The response is seen to be highly variable between individuals in that some individuals spawn out almost completely whereas others spawn only partially. Groups injected with supra-oesophageal ganglion homogenate prepared from individuals maintained under ambient conditions or under conditions of winter photoperiod and temperature showed a response similar to that in individuals described above. Groups injected with supra-oesophageal ganglion homogenate prepared from individuals maintained under summer conditions, or under conditions of winter photoperiod and summer temperature showed a very low level of response or no spawning at all.

Observations on gonadotropin hormone activity in *Harmothoe imbricata.* — Fig. 3 shows the results of amino acid incorporation into ovaries of *Harmothoe imbricata* following organ culture for 96 h in the absence or presence of brain homogenate. Incubation of ovaries of *Harmothoe imbricata* during the development of the first cohort of oocytes (8 March 1991) in the presence of brain homogenate and heat treated brain homogenate, and in medium (all containing $H^3$ leucine) shows enhanced uptake of the amino acid (ANOVA $F_{2,17} = 13.04$, $p=0.001$).

Source : MNHN, Paris

There is no difference observed on the degree of incorporation between ovaries cultured with fresh or heat-treated brain homogenate.

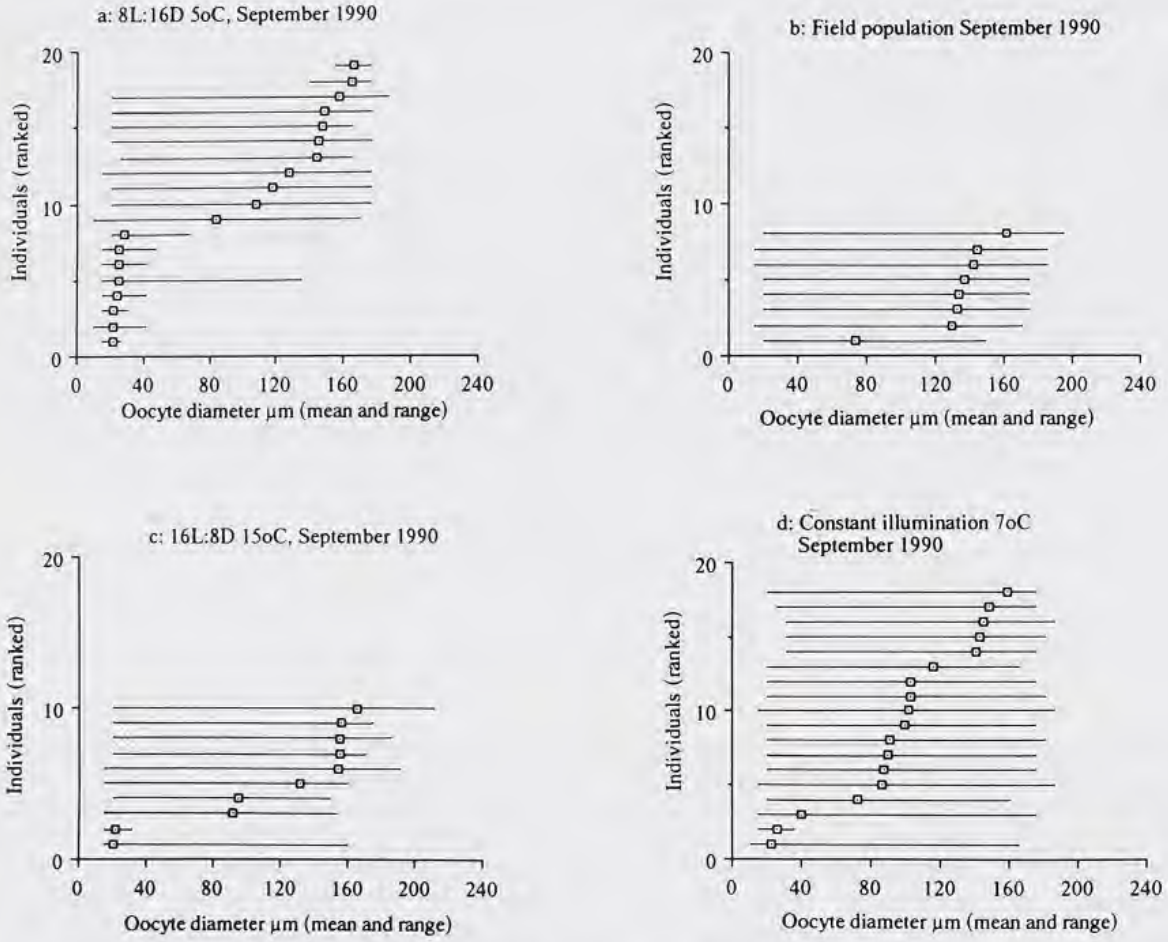



FIG. 1. — Oocyte diameters (means and ranges) in individuals of *Nephtys hombergii* which have been maintaind for a period of six months in the laboratory, and from the field in September 1990. The treatment groups were: a) maintained under a 8L:16D photoperiodic regime at 5°C, b) field collected animals, c) maintained under a 16L: 8D photoperiodic regime at 15°C, d) maintained under constant illumination at 7°C. It should be noted that, following spawning failure in the spring, individuals collected from the field in September still posess vitellogenic oocytes in the coelom.

Incubation of ovaries during the development of the second cohort of oocytes (29 April 1991) in the presence of brain homogenate prepared either from supra-oesophageal ganglia excised during development of the first or second oocyte cohorts also show enhanced uptake of the amino acid compared to the controls (ANOVA $F_{2,17} = 4.07$, $p=0.039$) but there is no significant difference between the two brain homogenate treatments. This demonstrates quite clearly the effect of gonadotropin hormone on ovaries during the development of both the first and second oocyte cohorts.

## DISCUSSION

The reproductive cycle of *Nephtys hombergii* is known to be controlled by two reproductive hormones (a gonadotropin and a spawning hormone) which are supposed to be secreted in a cyclical manner during the annual reproductive cycle (OLIVE, 1976, OLIVE & BENTLEY, 1980; OLIVE *et al.*, 1985). It has also been reported that

Source : MNHN, Paris

*Nephtys hombergii* is seen to undergo periodic spawning failure which may have an adaptive significance (OLIVE *et al.*, 1981). These spawning failures may occur in one of two ways: the production of a cohort of normal oocytes which are not released as a result of failure to secrete spawning hormone, or the premature resorption of gametes prior to the breeding season. It has been proposed that spawning failure and oocyte resorption may occur in response to 'poor condition' of the individual (measured by energy levels in the soma) (OLIVE *et al.*, 1985). The endocrine system is the means by which environmental (and somatic energy level) information is likely to be transduced. The results reported here on *Nephtys hombergii* suggest that photoperiod may influence the rate of oocyte resorption in unspawned oocytes and the onset of renewed gametogenesis. Short photoperiod appears to accelerate this process. Temperature does not appear to exert a marked effect. Photoperiod provides an accurate means of determining the timing of reproduction (BENTLEY & PACEY, 1992) whereas temperature cycles are less predictable and are variable from year to year.

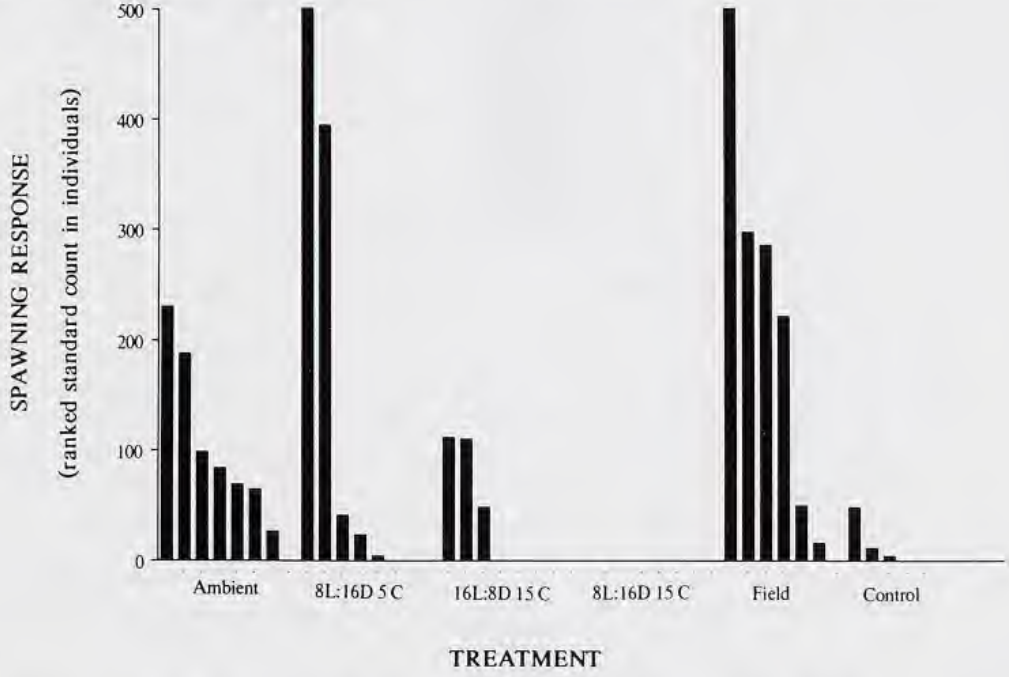



FIG. 2. — Spawning response in *Nephtys hombergii* injected with supra-oesophageal ganglion homogenate which had been obtained from individuals which had been maintained in the laboratory for a period of 219 days (from prior to the winter solstice) under: a) ambient photoperiod and temperature, b) a 8L:16D photoperiodic regime at 5°C, c) a 16L: 8D photoperiodic regime at 15°C, d) a 8L:16D photoperiodic regime at 15°C, or which had been obtained from individuals recently collected from the field. Control injected animals recieved a dose of 10µl of filtered seawater (solvent vehicle). Standard counts were those as used by OLIVE and BENTLEY (1980).

Observations on the production of spawning hormone in *Nephtys hombergii* show a rather different pattern. Prolonged exposure to short photoperiod alone is not sufficient to induce production of the hormone in the supraoesophageal ganglion. Low temperature, in contrast appears to induce spawning hormone production. Clearly production of spawning hormone is not critical in the timing of reproduction (only the timing of release plays a role in this respect), and temperature, therefore, may be an appropriate way of ensuring SH production. Observations on the field spawning of *Nephtys caeca* (BENTLEY *et al.*, 1984), and *Nephtys hombergii* may be similar, suggest that temperature may act as a 'trigger' for spawning. Temperature has been shown to play a role in controlling spawning of Nereidae (GOERKE, 1984) in which there are temperature "windows" for the swarming of species which are related to their geographical range. It is clear that the control of gametogenesis, hormone production and readiness to spawn in *N. hombergii* is a complex process in which temperature and photoperiod both appear to be involved.

There are few polychaete species in which both environmental and endocrine control of reproduction have been demonstrated. FRANKE (1983) has demonstrated the transduction of environmental information by the endocrine system of *Typosyllis prolifera* in an elegant series of experiments, but there are at present no other well

Source : MNHN, Paris

documented cases. The reproductive cycle of *Harmothoe imbricata* is controlled in a sophisticated manner by environmental factors, of which photoperiod is the most important (GARWOOD & OLIVE, 1978, 1982; GARWOOD ,

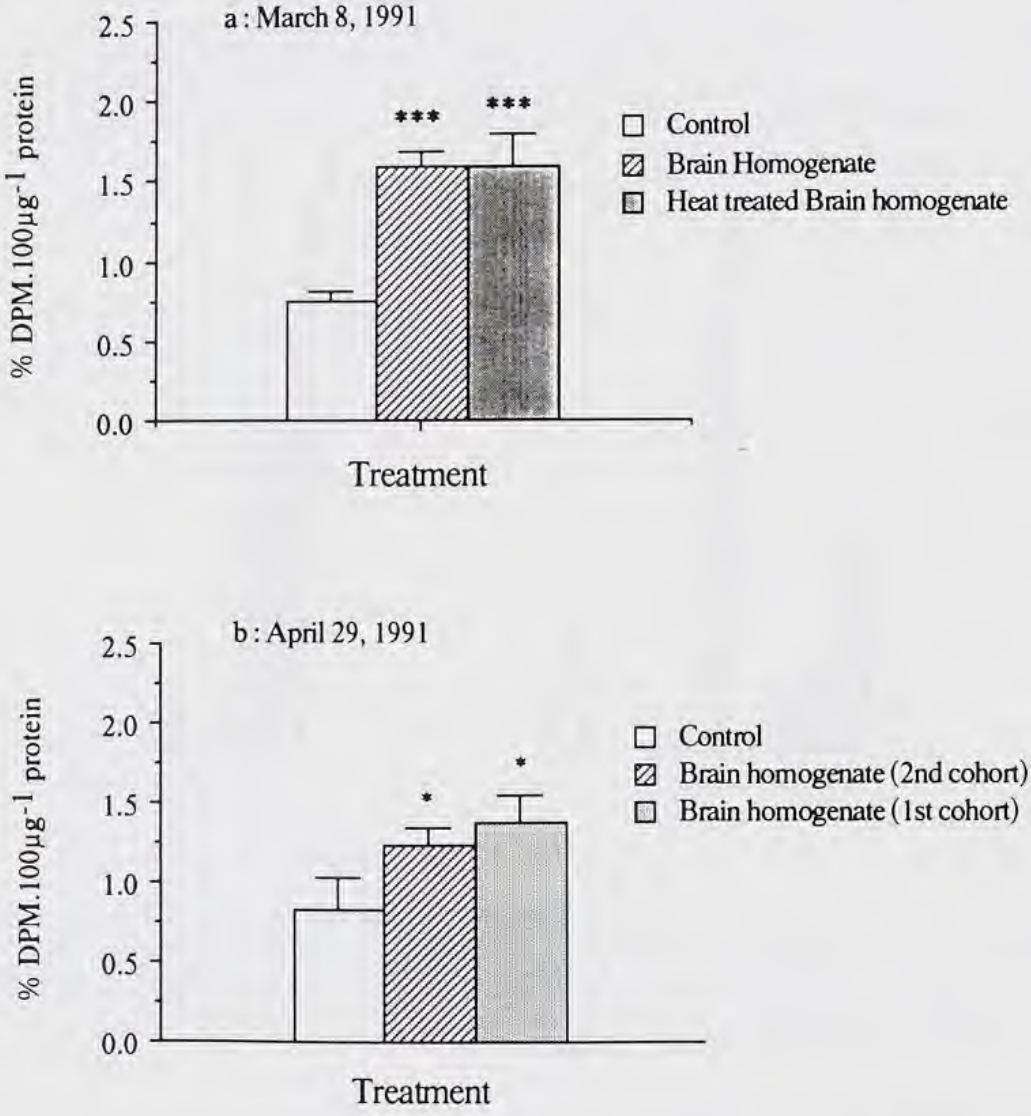



FIG. 3. — Incubation of ovaries of *Harmothoe imbricata* during: a) the development of the first cohort of oocytes (8 March 1991) in the presence of brain homogenate and heat treated brain homogenate, and in medium (all containing L-[4,5-$H^3$] leucine) and b) the development of the second cohort of oocytes (29 April 1991) in the presence of brain homogenate, prepared either from supra-oesophageal ganglia excised during development of the first or second oocyte cohorts, and in medium only.

1980; CLARK, 1988). Photoperiod acts to promote gametogenesis and to prevent abortion of the developing first cohort of oocytes (CLARK, 1988), and this information is relayed to the developing oocytes, at least in part, by a gonadotropin hormone (OLIVE *et al.*, 1990). The second cohort of oocytes, which develops independently of continued environmental input, we have demonstrated to be still under the gonadotropin hormone support. It may

Source : MNHN, Paris

be that once gonadotropin hormone secretion is switched on and the critical exposure to short days has been passed, secretion of the gonadotropin hormone cotinues throughout the development of the two oocyte cohorts.

## ACKNOWLEDGEMENTS

The authors are grateful to Dr. Marianne Ghyoot for checking the French abstract. This work was supported by a Natural Environment Research Council grant (GR3/6841) to MGB.

## REFERENCES

BENTLEY, M.G. & PACEY, A.A., 1992. — Physiological and environmental control of reproduction in polychaetes. *Oceanogr. Mar. Biol. Ann Rev.*, **30** : 443-481.

BENTLEY, M.G. & OLIVE, P.J.W., 1982. — An *in vitro* assay for gonadotrophic hormone in the Polychaete *Nephtys hombergii* Sav. (Nephtyidae). *Gen. Comp. Endocrinol.*, **47** : 467-474.

BENTLEY, M.G., OLIVE, P.J.W., GARWOOD, P.R. & WRIGHT, N.H., 1984. — The spawning and spawning mechanism of *Nephtys caeca* (Fabricius, 1780) and *Nephtys hombergi* Savigny, 1818 (Annelida: Polychaeta). *Sarsia*, **69** : 63-68.

BRADFORD, M.M., 1976. — A rapid and sensitive method for the quantification of microgram quantities of proteins using the principle of protein dye binding. *Anal. Biochem.*, **72** : 248-254.

CLARK, S., 1988. — A two phase photoperiodic response controlling the annual gametogenic cycle in *Harmothoe imbricata* (L.) (Polychaeta: Polynoidae). *Invertebr. Reprod. Dev.*, **14** : 245-266.

DALY, J.M., 1972. — The maturation and breeding biology of *Harmothoe imbricata* (L.) (Polychaeta: Polynoidae). *Mar. Biol.* **12** : 53-66.

DALY, J.M., 1974. — Gametogenesis in *Harmothoe imbricata* (Polychaeta: Polynoidae). *Mar. Biol.*, **25** : 35-40.

FRANKE, H.-D., 1983. — Endocrine mechanisms mediating light-temperature effects on male reproductive activity in *Typosyllis prolifera* (Polychaeta, Syllidae). *Wilhelm Roux' Arch. Dev. Biol.*, **192** : 95-102

GARWOOD, P.R., 1980. — The role of temperature and daylength in the control of the reproductive cycle of *Harmothoe imbricata* (L.) (Polychaeta: Polynoidae). *J. Exp. Mar. Biol. Ecol.*, **47** : 35-53.

GARWOOD, P.R., 1981. — Observations of the developing female germ cell in the polychaete *Harmothoe imbricata* (L.). *Int. J. Invertebr. Reprod.*, **3** : 333-345.

GARWOOD, P.R. & OLIVE, P.J.W., 1978. — Environmental control of reproduction in the polychaetes *Eulalia viridis* and *Harmothoe imbricata*. *In*: D.S. MCLUSKY & A.J. BERRY (eds), *Physiology and Behaviour of Marine Organisms*. Pergamon Press, Oxford, New York : 331-339.

GARWOOD, P.R. & OLIVE, P.J.W., 1982. — The influence of photoperiod on oocyte growth and its role in the control of the reproductive cycle of the polychaete *Harmothoe imbricata* (L.). *Int. J. Invertebr. Reprod.*, **5** : 161-165.

GOERKE, H.,1984. — Temperature dependence of swarming in North Sea Nereidae. *In*: A. FISCHER & H.-D. PFANNENSTIEL (eds), Polychaete Reproduction. *Fortschr. Zool.*, **29** : 39-44.

OLIVE, P.J.W. 1976. — Evidence for a previously undescribed spawning hormone in *Nephtys hombergii* (Annelida: Polychaeta). *Gen comp. Endocrinol.*, **28** : 454-460.

OLIVE, P.J.W., 1978. — Reproduction and annual gametogenic cycle in *Nephtys hombergii* and *N. caeca* (Polychaeta: Nephtyidae). *Mar. Biol.*, **46**: 83-90.

OLIVE, P.J.W. & BENTLEY, M.G., 1980. — Hormonal control of oogenesis, ovulation and spawning in the annual reproductive cycle of the polychaete *Nephtys hombergii* Sav. (Nephtyidae). *Int. J. Invertebr. reprod. Dev.*, **2** : 205-221.

OLIVE, P.J.W., BENTLEY, M.G., WRIGHT, N.H. & MORGAN, P.J., 1985. — Reproductive energetics, endocrinology and population dynamics of *Nephtys caeca* and *N. hombergi*. *Mar. Biol.*, **88**: 235-246.

OLIVE, P.J.W., CLARK, S. & LAWRENCE, A., 1990. — Global Warming and Seasonal Reproduction: Perception and Transduction of Environmental Information. *In*: M. HOSHI & O. YAMASHITA (eds), *Advances in Invertebrate Reproduction*. Volume **5.** Elsevier, Amsterdam, pp. 265-270.

OLIVE, P.J.W., GARWOOD, P.R. & BENTLEY, M.G., 1981. — Oosorption and reproductive failure in Polychaeta in relation to their reproductive strategy. *Bull. Soc. Zool. Fr.*, **106** : 263-268.

OLIVE, P.J.W. & LAWRENCE, A., 1990. — Gonadotrophic hormone in Nephtyidae (Polychaeta: Annelida): Stimulation of ovarian protein synthesis. *Invertebr. Reprod. Dev.*, **18**: 189-196.

Source : MNHN, Paris

Source : MNHN, Paris

# Morphometric analysis of cellular specification in *Platynereis* and *Pomatoceros* embryogenesis (Annelida, Polychaeta)

*Adriaan W.C. DORRESTEIJN & Craig Marc LUETJENS*

Zoologisches Institut (Abteilung 1) der Universität Mainz
Saarstraße 21, D-55099 Mainz, Germany

ABSTRACT

Despite differences in size and yolk content, the eggs of two sibling species, *Platynereis dumerilii* and *P. massiliensis*, show the same asymmetrical mode of cytoplasmic segregation. The largest part of the yolk-free cytoplasm is shunted into the D-quadrant after second cleavage. The specific cleavage behavior of the D-cell-line suggests a causal relation between cytoplasmic specification, speed of cell cycles and determination. We have expanded our morphometric analysis to the development of *Pomatoceros triqueter*, a polychaete with equal cleavage. However, we show that small though significant size difference between the quadrants may foreshadow the future dorsoventral polarity of this embryo. The largest quadrant cleaves asynchronously with respect to the other three quadrants. As in *Platynereis*, the speed of cell cycles of blastomeres are positively correlated with the volume of cytoplasm.

RÉSUMÉ

**Analyse morphométrique de spécification des cellules de *Platynereis* et *Pomatoceros* (Annélide Polychète)**

Malgré des différences de taille et de contenu de vitellus, les oeufs des deux espèces proches, *Platynereis dumerilii* et *P. massiliensis*, montrent le même mode de diversification cytoplasmique. La majeure partie du cytoplasme clair et sans vitellus est répartie dans le quadrant D après le deuxième clivage. Le comportement spécifique de clivage de la lignée cellulaire D suggère une relation entre la spécification cytoplasmique, la vitesse des cycles cellulaires et la détermination. Nous avons élargi l'analyse au développement de *Pomatoceros triqueter*, polychète à segmentation égale. Pourtant nous pouvons montrer que des différences minimes bien que significatives de taille entre les quadrants seraient indicatrices de la future polarité dorsoventrale de cet embryon. Le quadrant le plus large se divise asynchroniquement par rapport aux trois autres. Comme chez *Platynereis*, les vitesses des cycles cellulaires sont reliées positivement au volume du cytoplasme.

## INTRODUCTION

Embryogenesis in polychaetous annelids is regarded as a textbook example of determinative development. In many such eggs, structural animal-vegetal polarity is apparent before fertilization and foreshadows the future

DORRESTEIJN, A.W.C. & C.M. LUETJENS, 1994. — Morphometric analysis of cellular specification in *Platynereis* and *Pomatoceros* embryogenesis (Annelida, Polychaeta). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 45-50. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

antero-posterior axis of the trochophore larva. Even in seemingly apolar eggs this first body-axis is set up shortly after fertilization (KLUGE, 1991). Apart from the emergence of polar bodies which mark the animal pole, polarity is also manifested by ooplasmic segregation leading to a polar distribution of cytoplasmic components.

In nereids, the second body-axis, i.e. the dorsoventral axis, is believed to be set up at first cleavage (WILSON, 1892). In *Platynereis dumerilii*, the first cleavage produces two daughter blastomeres of unequal size: the small AB blastomere (27% of the total egg volume) and the larger CD blastomere. DORRESTEIJN (1990) was able to show that the cytoplasmic composition of these two cells differs as well. Volumetric analysis revealed that approximately 80% of the yolk-free cytoplasm, which accumulates at the animal pole prior to first cleavage, is allocated to the large CD blastomere, despite the fact that this blastomere includes only 73% of the total egg volume. Experiments in which we have equalized these volumetric proportions led to a duplication of dorsoventral polarity, and of the trunk structures of the young worm (DORRESTEIJN, BORNEWASSER & FISCHER, 1987). These data thus support the idea that the establishment of the dorsoventral axis depends on the differential distribution of both volume and cytoplasmic contents between the first two blastomeres.

In the present paper, we describe the developmental principles encountered in the unequally cleaving embryos of two sibling species of *Platynereis* and in the equally cleaving embryo of the serpulid *Pomatoceros triqueter*. Our results indicate that the creation of cytoplasmic asymmetry among the four embryonic quadrants may set up dorsoventral polarity even in "equally" cleaving polychaetes. The data also suggest a correlation between cytoplasmic distribution and cell cycle duration in individual blastomeres.

## MATERIALS AND METHODS

*Platynereis dumerilii* and *Platynereis massiliensis* were kept in laboratory cultures (HAUENSCHILD & FISCHER, 1969) at 18°C. The serpulid, *Pomatoceros triqueter*, was collected from the seabed round Helgoland. For *Platynereis dumerilii*, the mode of fertilization was previously described by DORRESTEIJN (1990). Fertilized eggs from *P. massiliensis* were collected from brood tubes in culture dishes. To induce spawning in *Pomatoceros* the calcareous tubes in which the animals live were opened with sturdy tweezers at the narrow, rear end. Subsequent agitation of the animal's tentacles made them crawl backwards by which they exposed themselves at the artificial hatch in the tube. Males (with pale abdomen) and females (with red abdomen) were put into separate bowls of seawater and started spawning spontaneously. The eggs were washed in seawater several times and were then fertilized with diluted sperm.

A careful estimate of cell cycle duration of individual blastomeres was achieved by evaluating several video-time-lapse recordings of the development (at 18 °C) of each of the three polychaetous species.

Procedures to collect morphometric data from serial sections (1 µm) were as described by SCHNEIDER, FISCHER & DORRESTEIJN (1992). For the small *Pomatoceros* embryos, however, we digitized every second 1 µm section in serial sections.

## RESULTS AND DISCUSSION

An intricate combination of pre-cleavage cytoplasmic segregation and unequal first cleavage during normal development of *Platynereis dumerilii* creates daughter-blastomeres which differ both in size and in cytoplasmic composition. This seems an essential initial step to create and propagate cellular diversity in the nereid embryo. At second cleavage, the small AB blastomere divides equally and there is no sign of cytoplasmic diversification. The large CD blastomere which contains the bulk of yolk-free cytoplasm (see introduction), however, cleaves unequally and the largest part of this yolk-free cytoplasm is shunted into the D-quadrant. As a result of this cleavage strategy, the D-cell obtains 60 % of the yolk-free cytoplasm although it includes only 51% of the total egg volume. Again, the cleavage introduces inequality in blastomere size and simultaneously regulates the cytoplasmic composition of the daughter blastomeres with a disproportional increase of yolk-free cytoplasm in the largest cell, the D-blastomere. The cleavage pattern of the D-quadrant differs from that of the other quadrants. Two descendants of the D-cell-line, the somatoblasts 2d and 4d, are formed at fourth and sixth cleavage, respectively. Both somatoblasts are exceptionally large cells and contain yolk-free cytoplasm almost exclusively. DORRESTEIJN (1990) has shown a positive correlation between the amount of yolk-free cytoplasm and the speed of cell cycles for all blastomeres (Fig. 1). As a result of the allocation of yolk-free cytoplasm, these D-quadrant-derived cells, 2d and 4d, proliferate much more rapidly than comparable cells of other quadrants. The relatively long initial cell cycle of

Source : MNHN, Paris

2d compared to its precursor cell 1D and its progeny $2d^1$ and $2d^{11}$, despite the fact that it obtained a large amount of yolk-free cytoplasm, seems to be exceptional. DORRESTEIJN (1990) proposes that the interval between fourth and fifth cleavage may be elongated due to cellular interactions which imprint dorsoventral polarity at the 16-cell stage.

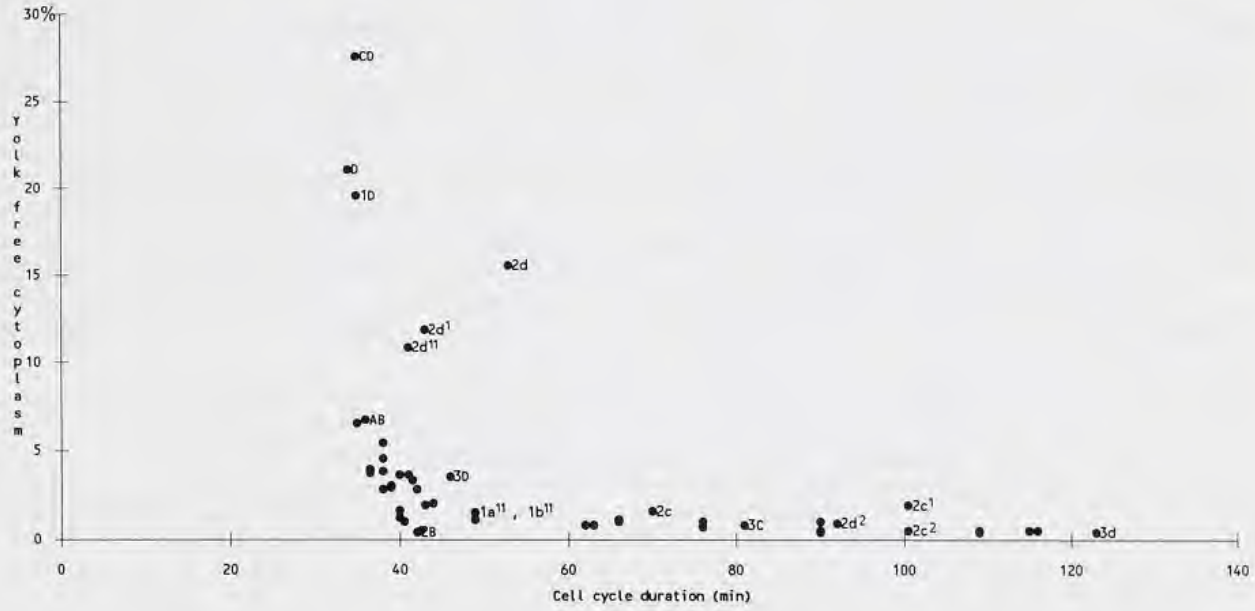



FIG. 1. — The amount of yolk-free cytoplasm in blastomeres of successive cleavage stages of *Platynereis dumerilii* is positively correlated with the rate of cell division. This diagram shows this correlation for the individual blastomeres. We have labeled some of the data points to show that CD and D-quadrant-derived cells proliferate more rapidly than other cells. However, cell cycles last longer after cells (even in the D-quadrant, e.g. $2d^2$ and 3d) have lost most of their clear cytoplasm.

Recently, we were able to show experimentally that the cleavage characteristics normal to a D-quadrant can also be observed in more than one quadrant if such quadrants contain sufficient yolk-free cytoplasm (DORRESTEIJN & EICH, 1991).

The eggs of the sibling species, *P. massiliensis*, are structurally polar from the start and extremely yolky. They have more than 10 times the volume and develop nearly four times slower than the eggs of *P. dumerilii*. Should the mode of cytoplasmic diversification found and documented by morphometric data for *P. dumerilii* be essential for determination of blastomeres, one would expect the development of this closely related species to follow essentially the same mode, even though the initial properties of such eggs are not the same. We have compared our data (SCHNEIDER, FISCHER & DORRESTEIJN, 1992) with early light microscope observations on the development of this species (WISTINGHAUSEN, 1891), which was then called the "nereidogenic form of *Nereis dumerilii*". Unfortunately, W failed to observe certain cleavages which makes the comparison of his proposed cell lineage tree with our cell-lineage results impossible.

Our comparative analysis of early development gave interesting insights into the way blastomeres become cytoplasmically diverse. The difference in size between the AB and CD blastomeres of *P. massiliensis* is less than in *P. dumerilii*. The CD blastomere of *P. massiliensis* measures 65 % of the total egg volume, yet contains approximately 73 % of the total amount of yolk-free cytoplasm. Thus, cytoplasmic diversification at first cleavage is a feature common to both species. Unlike the development of *P. dumerilii*, second cleavage of *P. massiliensis* is unequal in both blastomeres. The allocation of the yolk-free cytoplasm to the daughter blastomeres of AB is

Source : MNHN, Paris

proportional to the volumes of these cells. Although A- and B-blastomeres differ in size, there is no cytoplasmic diversification between these blastomeres. The cleavage in CD, however, allocates the yolk-free cytoplasm in proportions deviating from the relative volumes of the daughter cells with the largest amount (54 % of the total) ending up in the D-blastomere, which represents only 45 % of the total egg volume. Again, the cytoplasmic diversification of the D-quadrant is accomplished by both sibling species. The cytoplasmic specification of the D-cell-line is followed by a specific cleavage behavior differing in many respects from the other three quadrants. As in *P. dumerilii*, the somatoblasts 2d and 4d are large cells, receive almost exclusively yolk-free cytoplasm and proliferate more rapidly. Although cell cycles are nearly four times longer in *P. massiliensis*, a time scale transformation (Fig. 3 from SCHNEIDER, FISCHER & DORRESTEIJN, 1992) shows that the asymmetries in the sequence of divisions among both species are similar in all cell lines. In the same paper, the developmental similarity has been confirmed by reconstructions of embryos and shows that the asynchronies of blastomere proliferation, a result of differing cell cycle durations, can, with a few exceptions, be correlated with the allotments of yolk-free cytoplasm to the blastomeres of *P. massiliensis* as well. The stringency of cytoplasmic allocation in the two species suggests a causal relation between cytoplasmic specification and determination of the D-quadrant.

We have expanded our morphometric analyses onto the development of the serpulid *Pomatoceros triqueter*. The small (60-70 µm in diameter) egg of this polychaete contains only small amounts of yolk. The essentials of development were described by von DRASCHE (1884) and revised by GROEPLER (1986). According to these authors, the first and second cleavage are equal and the quadrants develop in radial symmetry. Thus, although differences in size and composition of the quadrants allow us to identify the quadrants in nereids, identification of quadrants seems impossible at early stages of *Pomatoceros*.

However, our own studies of the development of this small serpulid, partially reviewed by DORRESTEIJN & FISCHER (1988) showed that the blastomeres do not cleave synchronously. Even the second cleavage is slightly asynchronous in the first two cells, although the interval is less than a minute. Cleavage asynchrony is maintained

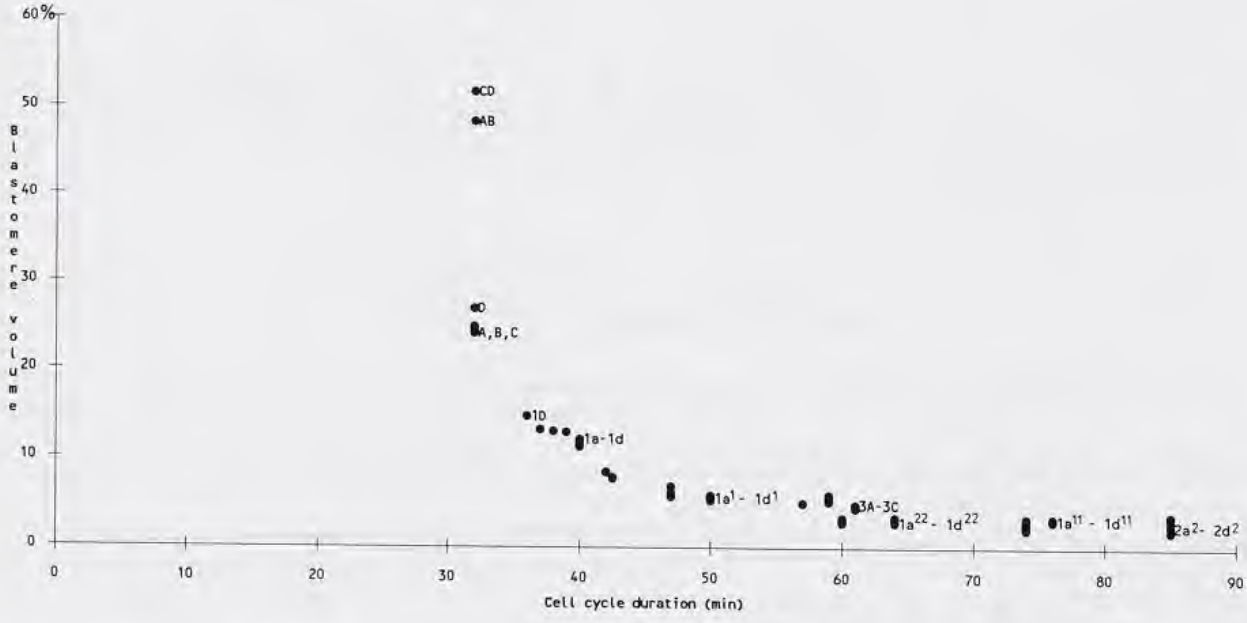



FIG. 2. — In *Pomatoceros triqueter*, blastomeres of successive cleavage stages which were studied up the 32-cell-stage show a positive correlation between the amount of cytoplasm and the rate of cell division. Since the yolk is distributed homogeneously within the cytoplasm, the blastomere volumes can be used as a measure of the amount of yolk-free cytoplasm.

Source : MNHN, Paris

and becomes more pronounced at later stages, especially among the macromeres and the different quartets of cells along the animal-vegetal axis. Morphometry of sectioned and reconstructed embryos shows small, yet statistically significant size differences between the blastomeres as early as at the two cell stage. The largest cell, which we shall call CD (according to the rules for the majority of unequally cleaving spiralians), is larger than AB by 3.5% (SD=1.3%; n=9) of the total egg volume. At the four cell stage, one of the daughter cells of CD is larger than the other daughter cell by little more than 2%, and larger than the daughter cells of AB by 3% (SD=1.9%; n=9). The size differences are maintained in the vegetal macromeres, but eliminated in the quartets of micromeres which are formed towards the animal pole during the third and subsequent cleavages.

Light microscope investigations of living embryos and morphometric analysis of serially sectioned embryos resulted in a clear and positive correlation between the sizes of individual blastomeres and the rate of cell division. From the diagram Fig. 2 it becomes clear that once the blastomeres grow smaller cell cycle duration increases. The first quartet of micromeres (1a-1d) divides nearly equally and the daughter cells, $1a^1$-$1d^1$, have cell cycles which are nearly 20 min longer than those of the mother cell. Since the yolk remains distributed homogeneously throughout the cytoplasm of the blastomeres, blastomere size must be proportional to the content of yolk-free cytoplasm in the blastomeres, and we can postulate the same correlation between the amount of yolk-free cytoplasm and the rate of cell division that we had previously found for *P. dumerilii*. This supports the idea that the small though significant size differences between the cells of the *Pomatoceros* 4-cell stage may cause the asynchronous development of its quadrants, which is reinforced in the macromeres at later stages. This asynchrony in the development of otherwise equivalent blastomeres introduces a polarity axis perpendicular to the preexisting animal-vegetal polarity which may well coincide with a dorsoventral axis which, however, has not yet been rigorously demonstrated in *Pomatoceros* embryos. For this reason we are studying the development of *Pomatoceros* beyond the stages we have investigated so far and focussing on the development of mesodermal stem cells which is a developmental aspect limited to the D-quadrant only. Should both mesoderm development and precocious cleavage in one of the quadrants be correlated aspects of development, setting up of cleavage asynchronies might prove an important factor to acquire blastomeres with different developmental fate.

## ACKNOWLEDGEMENTS

The careful maintenance of the animal stocks by Mr.A. HEINEN is gratefully acknowledged. The supply of the animals was made possible by the Laboratoire Arago (Banyuls-sur-Mer, France) and the Biologische Anstalt Helgoland (Helgoland, Germany). The collection of data for this paper would have been impossible without the financial support from the Deutsche Forschungsgemeinschaft, Bonn (grant Do 339/1-2).

## REFERENCES

DORRESTEIJN, A.W.C., 1990. — Quantitative analysis of cellular differentiation during early embryogenesis of *Platynereis dumerilii*. Wilhelm *Roux' Arch. Dev. Biol.*, **199** : 14-30.

DORRESTEIJN, A.W.C., BORNEWASSER, H. & FISCHER, A., 1987. — A correlative study of experimentally changed first cleavage and Janus development in the trunk of *Platynereis dumerilii* (Annelida, Polychaeta). *Wilhelm Roux' Arch. Dev. Biol.*, **196** : 51-58.

DORRESTEIJN, A.W.C. & EICH, P., 1991. — Experimental change of cytoplasmic composition can convert determination of blastomeres in *Platynereis dumerilii* (Annelida, Polychaeta). *Wilhelm Roux' Arch. Dev. Biol.*, **200** : 342-351.

DORRESTEIJN, A.W.C., FISCHER, A., 1988. — The process of early development. *In*: W. WESTHEIDE & C.O. HERMANS (eds), The Ultrastructure of Polychaetes. *Microfauna Marina , Gustav Fischer, Stuttgart*, **4** : 335-352.

DRASCHE, R. von, 1884. — Entwicklung von *Pomatoceros triqueter* L. *Beiträge zur Entwicklung der Polychaeten*, Heft 1 : 1-10, Wien, published privately.

GROEPLER, W., 1986. — Die Entwicklung bei *Pomatoceros triqueter* L. (Polychaeta, Serpulidae) vom befruchteten Ei bis zur schwimmenden Blastula. *Zool. Beitr. N. F.*, **29** : 157-172.

HAUENSCHILD, C. & FISCHER, A., 1969. — Platynereis dumerilii. *Mikroskopische Anatomie, Fortpflanzung, Entwicklung. Großes Zoologisches Praktikum*, Heft 10b. Gustav Fischer Verlag, Stuttgart, 1-55.

Source : MNHN, Paris

KLUGE, B., 1991 — *Cytologische Analyse der frühesten Entwicklungsvorgänge bei Platynereis dumerilii (Annelida, Polychaeta)*. Thesis, University of Mainz, 245 pp.

SCHNEIDER, S., FISCHER, A. & DORRESTEIJN, A.W.C., 1992. — A morphometric comparison of dissimilar early development in sibling species of *Platynereis* (Annelida, Polychaeta). *Wilhelm Roux' Arch. Dev. Biol.*, **201** : 243-256

WILSON, E.B., 1892. — The cell-lineage of *Nereis*: A contribution to the cytogeny of the annelid body. *J. Morph.*, **6** : 361-480.

WISTINGHAUSEN, C. von, 1891. — Untersuchungen über die Entwicklung von *Nereis Dumerilii*. Ein Beitrag zur Entwicklungsgeschichte der Polychaeten. *Mitt. Zool. Stat. Neapel*, **10** : 41-74.

Source : MNHN, Paris

# Observations on reproduction and growth of *Sabella spallanzanii* (Polychaeta, Sabellidae) in the Mediterranean Sea

*Adriana GIANGRANDE & Angela PETRAROLI*

Dipartimento di Biologia
Università di Lecce
73100 Lecce, Italy

ABSTRACT

A year of observations on a population of *Sabella spallanzanii* is reported. *In situ* measurements of tube length and correlation of this parameter to other variables such as worm length and biomass gave indications on growth-rate. Reproduction was followed by monthly samples and examination of gonad maturation. Sex ratio and minimal size at reproduction were also investigated. In the Mediterranean Sea *S. spallanzanii* showed a fast growth-rate and reproduced during February. Oogenesis is of extraovarian type and eggs reach 250 µm. The presence of protandric hermaphroditism is indicated.

RÉSUMÉ

**Observations sur la reproduction et la croissance de *Sabella spallanzanii* (Polychaeta, Sabellidae) en Méditerranée**

Des observations sur la reproduction d'une population de *Sabella spallanzanii* ont été faites pendant une année. La longueur des tubes a été évaluée par des mesures directes des individus dans leur habitat naturel. Une corrélation entre la longueur de tube, la longueur du ver et la biomasse a pu être démontrée. A partir de ces corrélations, il est possible d'avoir une indication sur la croissance du ver. Des échantillons ont été récoltés tous les mois pour suivre la reproduction des individus. La taille minimale des vers à la reproduction et leur sex-ratio ont été calculés. La ponte de *S. spallanzanii* a lieu au cours de l'hiver en Méditerranée. La taille ovocytaire maximale observée a été de 250 µm. Néanmoins les premiers stades de la gamétogénèse n'ont pas été observés et des observations complémentaires sont nécessaires. L'espèce présente un hermaphroditisme protérandrique.

## INTRODUCTION

*Sabella spallanzanii* (Gmelin, 1791) is one of the most "popular" Mediterranean polychaetes. It has been used as an experimental animal in numerous studies, but almost always under the generic name of *Spirographis*.

Recently PERKINS and KNIGHT-JONES (1991) synonymized *Spirographis spallanzanii* Viviani with *Sabella*

GIANGRANDE, A. & A. PETRAROLI, 1994. — Observations on reproduction and growth of *Sabella spallanzanii* (Polychaeta, Sabellidae) in the Mediterranean Sea. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 51-56. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

*penicillus* Linnaeus, but suggested to suppress *penicillus* and other synonyms to stabilize the name *spallanzanii*.

They pointed out that the correct name for the species, *penicillus*, has frequently been used incorrectly for *Sabella pavonina* Savigny typical of northern Europe.

*Sabella spallanzanii* is common along the Italian coast. It can be found in the open sea from 1 to 30 m depth, as well as in shallow hard bottom areas of harbours, where it reaches high densities. Probably the open sea and the harbour forms belong to different ecotypes because their behaviour and resistance under laboratory conditions are different.

Despite its wide distribution, and its frequent use in physiological studies (IVANOV, 1908; FOX, 1938; KIORTSIS & MORAITOU, 1965; PARRINELLO & RINDONE, 1981), its reproduction and life-cycle are poorly known (MCEUEN *et al.*, 1983).

The role of coelomocytes in the maturation of germinal products in some specimens from Naples, which surely belonged to *Sabella spallanzanii*, was studied by DALES (1961). While the electron microscopical investigation on sperm of the species incorrectly referred as *Sabella penicillum* by GRAEBNER and KRYVI (1973), should probably be referred to *Sabella pavonina*.

The present paper deals with a year of observations on *in situ* growth and reproduction of a Mediterranean harbour population of *Sabella spallanzanii*.

## MATERIALS AND METHODS

The study was conducted at the Mar Grande of Taranto (Gulf of Taranto, Ionian Sea) along an artificial, vertical cliff. The individuals of *Sabella spallanzanii* were distributed in patches. One group measured 2 m deep and 9 m wide, and was chosen to follow individual growth. *In situ* measurements of tube length were done by Scuba divers for about one year. Tubes were measured within an area of 400 $cm^2$, using a plastic square to delimitate the surface. The tube length was correlated with other features of the worm.

Biomass was estimated as dry weight by drying individuals at 65°C for 24 h. Various sized specimens were collected monthly from the dense patch under study and from adjacent zones. Size at maturation and sex ratio were determined. Coelomic fluid was analyzed in the laboratory to examine for sexual maturation.

Specimens were fixed in 5 % glutaraldehyde buffered to pH 7.4 and post-fixed for one hour in 4 % osmium tetroxide for histological studies. For light microscopy, 1 µm thick sections were cut with a glass knife. Thin sections were cut on an ultramicrotome with a diamond knife for electron microscopy

The temperature cycle was typical of Mediterranean confined environments with a range of 11 °-29 °C. Salinity values were stable at approximately 38 P.S.U.

## RESULTS

DENSITY, GROWTH AND BIOMETRY. — Individuals of *Sabella spallanzanii* were located within a suspension feeder community typical of Mediterranean eutrophic zones such as harbours (TURSI *et al.*, 1985). At the beginning of the study in May 1991, only small individuals were present within the patch, and the density was about 300 ind. $m^{-2}$. The mean tube length in July 1991 was 10 cm (Fig. 1a). In April 1992 it was 18 cm, and in August 1992 it reached 20 cm in length (Fig 1b), with a density of about 150 ind. $m^{-2}$.

The tube length was correlated with the length of the worm (Fig. 2a), biomass (Fig. 2b) and the number of setigers (Fig. 2c). Biomass was estimated at 60 g. $m^{-2}$, and 75 g. $m^{-2}$ in July 1991 and August 1992, respectively.

The crown of *Sabella spallanzanii* is asymmetric, with one involute lobe having an arrangement of spiralled radioles, but spiralization is absent in small individuals (KNIGHT-JONES *et al.*, 1991). Correlation of number of spirals with length showed that worms up to 9 cm in length do not show any spiralling, whereas large specimens from 30 to 40 cm in length have up to 4 secondary spirals (Fig. 2d). The ratio of body length to crown increases with increasing body length, from 1.5 to 4.7, as observed for other species (GIANGRANDE, 1991).

## REPRODUCTION

As observed by DALES (1961), germinal products in sexually mature specimens are found in the coelomic cavity. No germinal products were observed in the coelom from May to July 1991. The content of the coelom was

Source : MNHN, Paris

bright orange or brown and had a rich creamy consistency due to the presence of large coelomocytes. These cells measure up to 70 µm in diameter. The peritoneum appeared hypertrophic in July, 1991. The early stages of

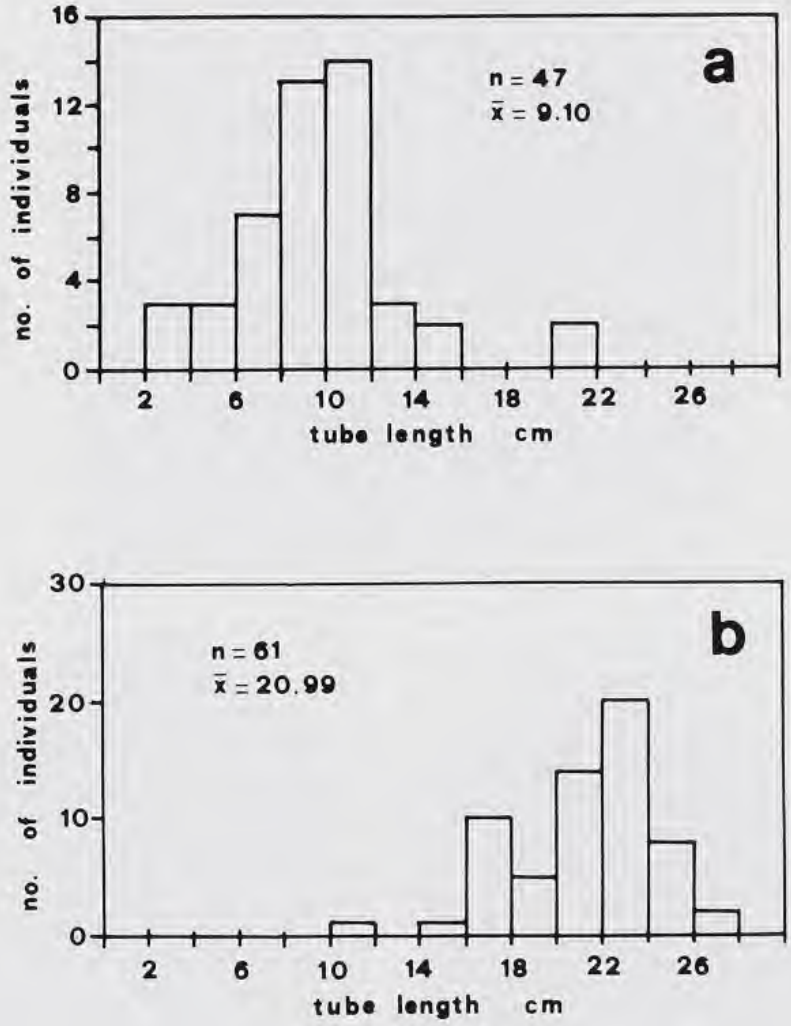



FIG. 1. — *Sabella spallanzanii*. **a**: Frequency histograms of tube length in July, 1991; **b**: Frequency histograms of tube length in August, 1992.

germinal products were probably present in August and September, but samples relative to this period were not obtained. Germinal products were well developed in October, 1991, when eggs measured about 100 µm. They reached about 200 µm in December, 1991, and males contained spermatids predominantly at an early stage of maturation. Eggs had completed vitellogenesis and measured 250 µm in January, 1992, (Fig. 3a), and ripe spermatozoa (Fig. 3b-c) together with late spermatid stages were present in the males. Spawning occurred in February. Some females still retained a few eggs surrounded by a large number of coelomocytes in March. The coelom of the worms was once again full of coelomocytes in April, 1992, and no germinal products were present. As observed by DALES (1961) the quantity of coelomocytes decreased as oocytes matured.

Source : MNHN, Paris

## SEX RATIO

The minimal size at maturation was computed as 15 cm in length. Specimens from 15 to 20 cm long were all males ; females occurred only in specimens greater than 20 cm long. The sex ratio was of 1 : 1 in individuals from 25 to 30 cm. However, males represented more than 80% of the reproductive population when all sized worm were considered.

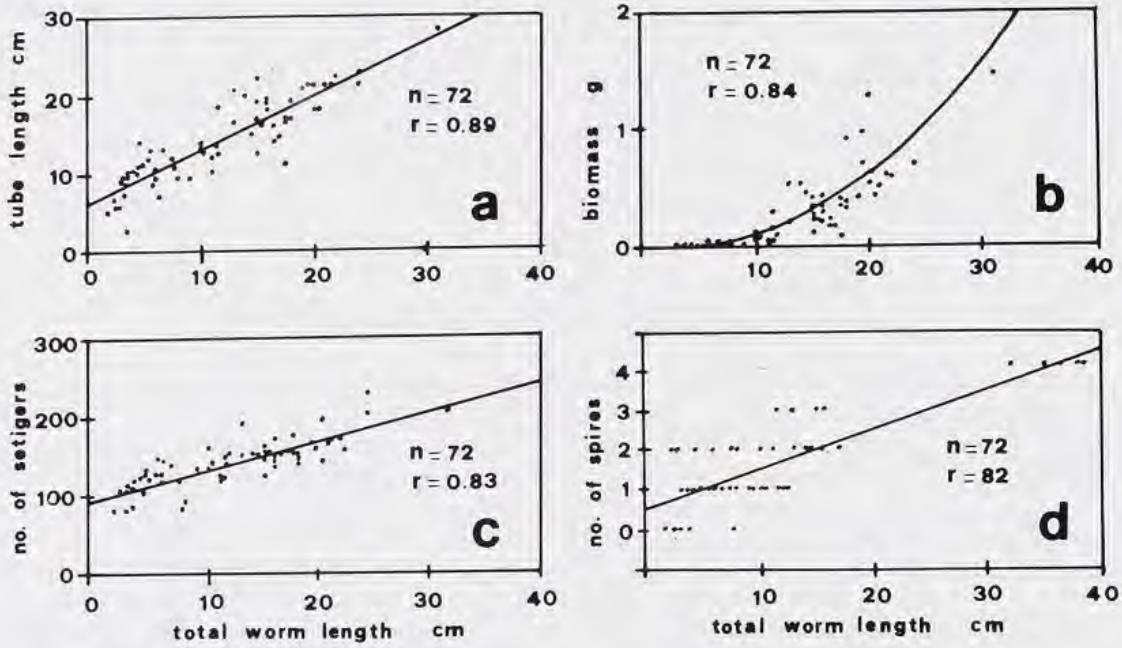



FIG. 2. — *Sabella spallanzanii*. **a**: Correlation between tube length and total worm length; **b**: Correlation between worm length and biomass (Dry weight); **c**: Correlation between worm length and number of setigers; **d**: Correlation between worm length and number of spirals of the branchial crown.

Individuals from the patch under observation with tubes measuring about 15 cm in length were all males. During the period of study no females were present within this patch. Females were found among larger individuals collected from adjacent zones.

## DISCUSSION AND CONCLUSION

*Sabella spallanzanii* is characterized by a rapid growth rate. Tube length doubled in 10 months. In the laboratory, it has been reared using many different food sources, and it can be hypothesized that it can feed also on particulate organic matter. Size distribution within the patch suggested that it could be the product of a single recruitment episode. The biomass computed per square meter was quite large, even thougth mortality seemed to be very high during the period of observation, since the density decreased from 300 to 150 ind. $m^{-2}$.

Spiralization of the radioles represents a growth strategy in large-sized sabellids. In this way they can obtain an efficient respiratory and feeding surface without elongation of the crown, diminishing the risk from predation. Correlation of the number of spirals with body length is important taxonomically, since one of the features used to distinguish *Spirographis* from *Sabella* was the presence of spiralization in the crown.

Reproduction in *Sabella spallanzanii* seems to be synchronized among individuals. According to DALES (1961), spawning occurs in winter. However, samples relative to this first year were not adequate to investigate the entire gametogenic cycle, especially concerning the appearance of the early stages of germinal development. Data of the present work suggests that gametogenesis begins in summer. During the gametogenesis, coelomocytes were observed to decrease in number, especially in females. After spawning the number of coelomocytes increases

Source : MNHN, Paris

rapidly and by spring fill the coelomic cavity. DALES (1961) reported that coelomic cells are organized as storage

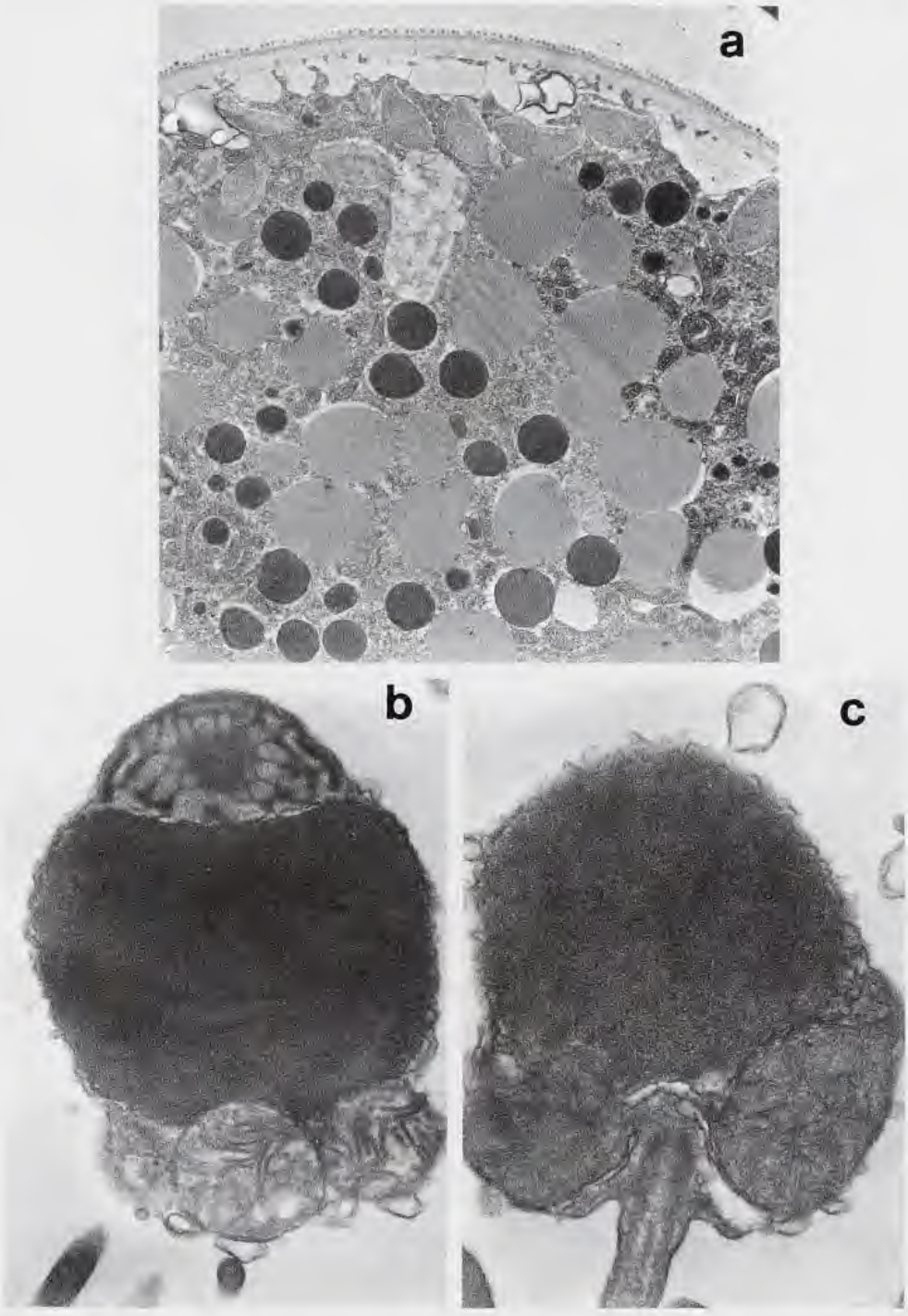



FIG. 3. — *Sabella spallanzanii*. **a**: Electron micrograph of a section through cortex of ripe egg, showing numerous yolk bodies, magnification 91,000; **b-c**: Electron micrograph through heads of ripe spermatozoa, magnification 52,000.

centres for the maturation of gametes. Coelomocytes are derived from the peritoneum as small actively phagocytic cells. Large coelomocytes eventually rupture and liberate their inclusions into the coelomic fluid to be taken up by

Source : MNHN, Paris

younger cells or by gametes. The oogenesis therefore is of the extraovarian type and is classified by ECKELBARGER (1983) as "with numerous amoebocytes".

The mature egg diameter is 250 µm ; therefore a lecithotrophic development can be hypothesized. Even thougth the egg diameter does not agree with that of other sabellids having a broadcaster reproductive pattern (MCEUEN *et al.*, 1983). The structure of spermatozoa is of the primitive type, adapted for external fertilization. It is of the ect-aquasperm type, which is the most common type among polychaetes. However, the sabellid ect-aquasperm type was classified by JAMIESON & ROUSE (1989) as neo-aquasperm, hypothesizing in some sabellids a re-evolution of ect-acquasperm from ent-aquasperm type. The sperm morphology is very similar to that described for *Sabella penicillum* (GRAEBNER & KRYVI, 1973), but this is probably a different species from *Sabella spallanzanii*.

Due to the problems existing in the taxonomy of *Sabella spallanzanii* (PERKINS & KNIGHT-JONES, 1991), some difficulties arise in comparing present data to other previous works. For example, *Sabella penicillus* is reported to be a dioecious species (MCEUEN, *et al.*, 1983), but current data, i.e. deviation in sex ratio from 1 : 1 and size of females, supports the hypothesis for the presence in *Sabella spallanzanii* of a protandric hermaphroditism, Probably the individuals examined by DALES (1961) were of large size and this led the author to consider the species as gonochoric. Further investigations are needed to confirm this hypothesis.

## REFERENCES

DALES, P.R., 1961. — The coelomic and peritoneal cell systems of some Sabellid Polychaetes. *Q. J. Microscop. Sci.*, **102** : 327-346.

ECKELBARGER, K.J., 1983. — Evolutionarly radiation in polychaete ovaries and vitellogenic mechanisms: their possible role in life-history patterns. *Can. J. Zool.*, **61** : 487-504.

FOX, M.H., 1938. — On the blood circulation and metabolism of sabellids. *Proc. Royal Soc.* (B), **125** : 554-569.

GIANGRANDE, A., 1991. — Behaviour, irrigation and respiration in *Eudistylia vancouveri* (Polychaeta, Sabellidae). *J. mar. biol. Ass. U.K.*, **71** : 27-35.

GRAEBNER, I. & KRYVI, H., 1973. — The spermiogenesis and mature sperm of *Sabella penicillum* (Polychaeta). An electron microscopical investigation. *Norw. J. Zool.*, **21** : 211-226.

IVANOV, P., 1908. — Regeneration des vorderen, und des hinteren Korperendes bei *Spirographis spallanzanii*. Viv. *Zeitschrift f. wissensch. zoologie.*, **91** : 510-558.

JAMIESON, B.G.M. & ROUSE, W., 1989. — The spermatozoa of the Polychaeta (Annelida): an ultrastructural review. *Biol. Rev.*, **64** : 93-157.

KIORTSIS, V. & MORAITOU M., 1965. — Factors of regeneration in *Spirographis spallanzanii*. *In:* V. KIORTSIS & H.A.L. TRAMPUSH (eds), *Regeneration in Animals and related problems*. North Holland Publ., Co., Amsterdam : 250-261.

KNIGHT-JONES, P., KNIGHT-JONES, W., & ERGEN, Z., 1991. — Sabelliform polychaetes, mostly from Turkey's Aegean coast. *J. Nat. Hist.*, **25** : 837-858.

MCEUEN, F.S., WU, B.L., & CHIA, F.S., 1983. — Reproduction and development of *Sabella media*, a sabellid polychaete with extratubular brooding. *Mar. Biol.*, **76** : 301-309.

PARRINELLO, N. & RINDONE, D., 1981. — Studies on the natural hemolytic system of the annelid worm *Spirographis spallanzanii* (Polychaeta). *Dev. Comp. Immun. N.Y.* **5** : 33-42.

PERKINS, T.H. & KINGHT-JONES, P., 1991. — Towards a revision of the genera *Sabella* and *Bispira* (Sabellidae). *Ophelia*, Suppl. **5** : 698.

TURSI, A., MATARRESE, A., CECERE, E. & RIBECCO, N., 1985. — Sviluppo di popolazioni bentoniche su pannelli fouling nel Mar Grande di Taranto. *Atti S.I.T.E.*, **5** : 585-589.

Source : MNHN, Paris

# The functional significance of blood plexuses in the ecology of *Ophelia bicornis* Savigny

*Tegwyn HARRIS*

Department of Biological Sciences
The University of Exeter, Hatherly Laboratories
Prince of Wales Road, Exeter, EX4 4PS, U.K.

ABSTRACT

The anatomy of the anterior blood vascular system of *Ophelia bicornis* is described with especial reference to its plexuses of inflatable blind capillaries. The functional significance of these plexuses under the influence of systolic blood pressure and their roles in the provision of an efficient burrowing mechanism through relatively dilatent sand whilst, at the same time, helping to maintain an efficient transport system for dissolved substances is described and discussed within the context of the ecology of the polychaete. The study has been carried out by direct observation of the living worm, by dissection and by analysis of absorbed radioactively-labelled glutamic acid.

RÉSUMÉ

**Signification fonctionnelle des plexus sanguins pour l'écologie d'*Ophelia bicornis* Savigny**

L'anatomie du système vasculaire sanguin antérieur d'*Ophelia bicornis* est décrite en considérant plus spécialement ses plexus de capillaires aveugles et dilatables. La signification fonctionnelle de ces plexus, sous l'influence de la pression sanguine lors de la systole, leur rôle dans la mise en oeuvre d'un mécanisme efficace pour l'enfouissement dans des sables relativement compacts et le rôle qu'ils jouent, dans le même temps, comme système de transfert des substances dissoutes, sont décrits et discutés dans le contexte de l'écologie du Polychète. L'étude a été conduite par observation directe d'animaux vivants, par dissection et par l'analyse d'acide glutamique radioactif absorbé.

## INTRODUCTION

The mechanisms of digging into, and travelling through, marine sediments by soft-bodied invertebrates has been studied at some length. Both in the bivalved molluscs (ANSELL & TRUEMAN, 1967; TRUEMAN, 1968) and in the annelids (CHAPMAN, 1950, 1958), it has been shown that effective locomotion is usually achieved by an interaction of the body-wall musculature and an internally-developed hydrostatic tension in a body fluid, usually that which fills the coelom.

The most extensive studies of burrowing in the Polychaeta have involved *Arenicola marina*. CHAPMAN and

HARRIS, T., 1994. — The functional significance of blood plexuses in the ecology of *Ophelia bicornis* Savigny. *In:* J.-C. DAUVIN, L. LAUBIER et D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 57-63. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

NEWELL (1947) and TRUEMAN(1966a,b) have discussed the nature and mode of action of the hydrostatic system, whilst WELLS (1944, 1952, 1954, 1961) has described the mechanical activities of the proboscis and their significance to the behaviour of the worm. The consensus of this work is that the primary thrusting force is generated by the interaction of the internal coelomic fluid pressure and the highly-controlled body- wall muscles and muscular, eversible proboscis.

WELLS (1954) and CHAPMAN (1958) pointed out that much of the success of this process is due to the presence in *Arenicola* of an open coelom which results in the deployment, at the anterior, of the total force generated by extensive areas of body-wall musculature reacting against a "whole-body" hydrostatic skeleton. In association with this, WELLS (1954) also suggested that the three retained anterior septa of *Arenicola* serve to resist the at-rest coelomic pressure in order to restrict unnecessary extension of the proboscis.*Ophelia bicornis*, too, has a coelom which is continuous throughout the body and two retained anterior septa, but they are used in a manner which is totally unlike that of *Arenicola*. This paper reports the mode of action of that coelomic apparatus and of the way in which it is augmented by the activities of the complex blood vascular system.

## MATERIALS AND METHODS

a. Anatomical and behavioural study.

*Ophelia bicornis* was collected from Bull Hill Bank in the estuary of the River Exe, Devon, U.K. Worms were killed and fixed by immersion for about three hours in 5% neutral formalin in sea water, some after fresh-water narcotisation, others without pre-treatment. This was necessary since, as reported by BROWN (1938) for *Ophelia rathkei*, the only agent which is effective for the narcotisation of *O. bicornis* is fresh water. Immersion in fresh water for about twenty minutes induces total narcosis and also causes the worm to extend to its full, straight, length. Since this is clearly induced by osmotic influx of water into the coelomic compartment, all dissections were performed on narcotised specimens for clarity and repeated on untreated specimens for confirmation of the exact state of the organs and tissues. In practice, it was found that even the most delicate coelomic capillaries were not modified by the fresh-water treatment.

Locomotory activities were observed in *Ophelia* provided with semi-transparent artificial sand composed of a mixture of glass beads of appropriate granularity moistened with sea water. Use of immature worms, with relatively unpigmented and thin body-walls, permitted a certain amount of direct observation of internal activity.

b. Amino acid uptake.

Amino acid uptake was investigated using L-[U-$^{14}$C] glutamic acid (50µCi. cm$^{-3}$), supplied by Amersham International, in a laboratory régime based upon "Analar" quality acid-cleaned sand and artificial sea water as formulated by DAWSON et al (1969).

132 µl of radioactive amino acid were added to 75ml of artificial sea water. This was thoroughly mixed and added to 150 g of sand and cooled to 10 °C. Experiments were carried out at this temperature. Sand prepared in this way was found to contain sufficient radioactive material to give 39 072 dpm. g$^{-1}$ sand at the degree of dampness used in the experiments (dpm = disintegrations. min$^{-1}$ as counted in the liquid scintillation counter).

*Ophelia bicornis* were placed in the prepared sand and allowed to burrow naturally.

Individual worms were removed at intervals of 10 min, 20 min, 30min, 45 min and 60 min, rinsed in artificial sea water and immediately cut into three portions representing the prostomial and pharyngeal region, the mid-gut (intestinal) region and the hind-gut (chiefly rectal) region. The mass of these portions was determined and they were prepared for liquid scintillation as follows.

The tissue was placed in glass scintillation vials with 0.9 ml of "Soluene 350" and digested at 40 °C overnight. After cooling to room temperature, 0.2 ml propan-1-ol and 0.4 ml 30 % hydrogen peroxide in two 0.2 ml portions over two hours, were added to decolorize the pigmented solution. After the addition of the second portion of hydrogen peroxide, the samples were heated to 40 °C to drive off excess peroxide and again allowed to cool.

5.0 ml "Packard 299" scintillation fluid were added to each vial and the activity of the mixture was measured in a Packard "Tri-carb 460 CD" liquid scintillation counter by the sample channels method against a quench curve prepared from measurement of vials containing "Packard 299" fluid with chloroform as the quench reagent.

c. Autoradiography.

Worms destined for autoradiographic study were allowed to ingest the radioactive amino acid-treated sand for two hours prior to fixation. This relatively lengthy treatment time was decided upon since the aim of the present

Source : MNHN, Paris

investigation was solely to determine the extent of amino acid uptake and its broad distribution within the tissues of *Ophelia bicornis*.

Worms were fixed in 3 % neutral formalin in sea water without prior narcotisation and, during fixation, were divided into 1.0 cm long portions so that the intestine could be cleared of sand. The fixed tissues were dehydrated through a standard ethanol series, embedded in paraffin wax and sectioned at 10µm. Sections were mounted on gelatin-subbed slides as recommended by Kodak Ltd (1978) and ROGERS (1979). They were coated with "Kodak" AR10 stripping film and allowed to expose, in the dark, at 15 °C for 14 days. The slides were developed in "Kodak" D-19 and fixed in "Kodak" F-5.

The *Ophelia* tissues acquired a pale straw colour during processing which rendered them clearly visible beyond the developed silver, thus obviating the need for staining.

Control of the technique was effected in two ways: a) by comparison with similarly- processed sections of tissues which had not been subjected to radioactive labelling and, b) by examination of putative developed silver grains by dark-field microscopy, as recommended by ROGERS (1979).

## RESULTS

a. The anterior coelom and its vascular system

The overall pattern of the blood vascular system followed the descriptions of CLAPARÈDE (1870) from *Ophelia radiata* and of BROWN (1938) from *O. rathkei*. The constructional design is in two major parts, a posterior system based upon a series of sinuses and an anterior system of complex blood vessels.

The whole length of the intestine of *O. bicornis* is surrounded by voluminous dorsal and ventral blood sinuses, of which the dorsal is the larger. The ventral sinus more nearly resembles an inflated blood vessel and, for most of its length, is virtually buried within the ventral tissues of the typhlosole.

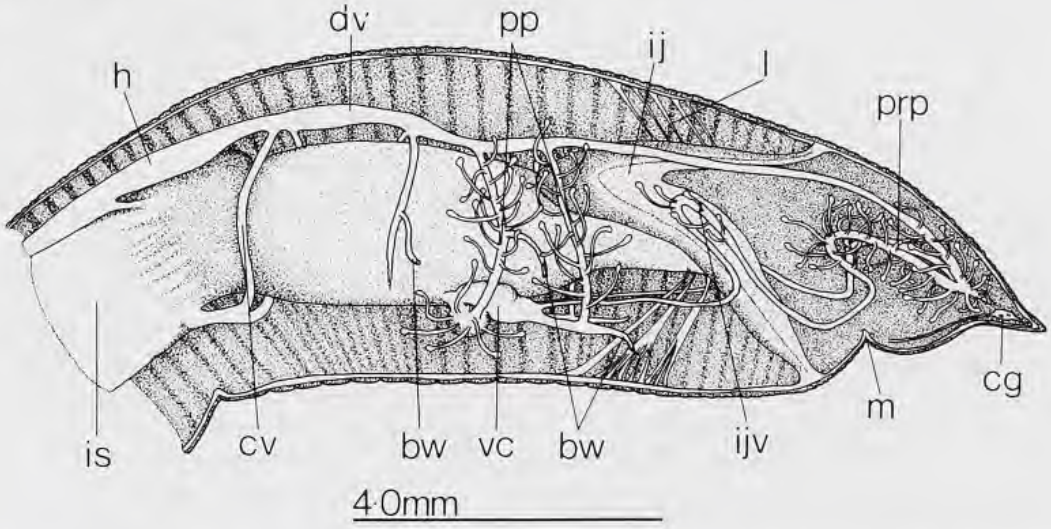



FIG. 1. — A semi-diagrammatic drawing of the anterior of *Ophelia bicornis* dissected from the right side and cut back to beyond the ventral nerve cord. For the sake of clarity the prostomial part of the pharynx is not shown. bw, vessels to the body-wall. - cg, cephalic ganglion. - cv, commissural vessel. - dv, dorsal blood vessel. - h, heart. - ij, "injector organ". - ijv, "injector organ" blood vessel. - is, intestinal sinus. - l, ligaments. - m, position of mouth. - pp, pharyngeal capillary plexus. - prp, prostomial capillary plexus. - vc, ventral cisterna.

The anterior blood system is illustrated semi-diagrammatically in Fig.1. The conspicuous parts of the system arise from the junction of the buccal chamber with the intestine (shown at the left of Fig.1). At this point, the dorsal intestinal sinus gives rise to a muscular heart which contains a non-return flap-valve (Fig.2). From the heart, an anterior dorsal vessel gives rise to four paired vessels. From posterior to anterior these are - a pair of lateral vessels which connect the dorsal and ventral sinuses, a pair of vessels which enter the wall of the buccal chamber, then two pairs of commissural vessels which link with a sub-pharyngeal cisterna of chambered

Source : MNHN, Paris

appearance. The dorsal vessel then passes through the walls of the "injector organ" to the prostomial coelom where it divides into two anterior lateral vessels which travel back through the "injector organ" wall, apparently between the two septal components, and continue as afferents to the sub-pharyngeal cisterna.

"Blind appendages" or, perhaps more correctly "blind capillaries", arise in large numbers from the anterior paired vessels, forming a dense plexus surrounding the pharynx and another within the prostomial coelom, as shown in Fig.1. Cardiac activity produces alternate swelling and deflating of the blind tips of the capillaries: at cardiac systole, 1.0 - 1.5mm of the tip swells to such an extent that the capillary wall stretches until it is virtually invisible under the low power of the microscope; at cardiac diastole, the tubular appearance is resumed.

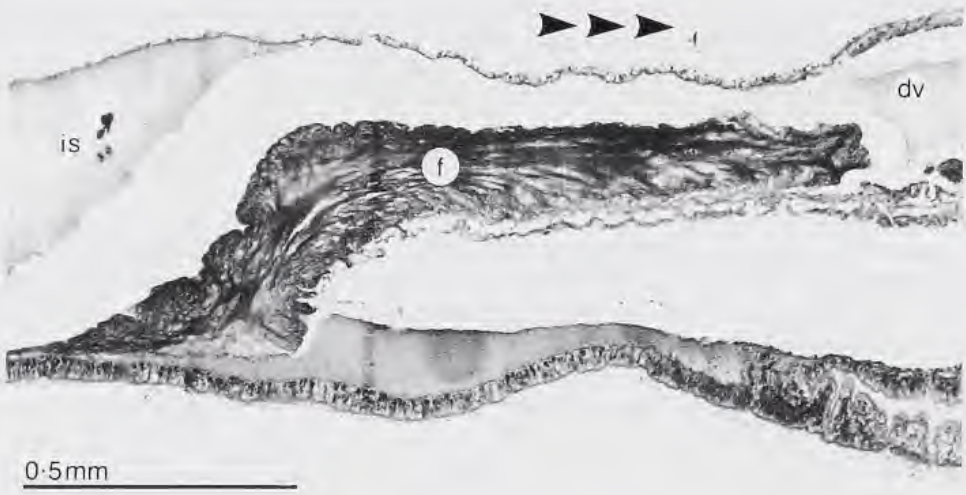



FIG. 2. — A median longitudinal section of the heart of *Ophelia bicornis*, - dv, dorsal blood vessel. - f, the flap valve. - is, intestinal sinus. The arrows point toward the anterior of the worm.

The increase in volume of the anterior blood system due to the simultaneous inflation of so large a number of blind capillaries is considerable. It seems that this activity is of benefit to *O.bicornis* in two ways.

The most obvious purpose of the mechanism is perhaps that of putting a large volume of blood, under pressure, in close contact with the coelomic fluid and its corpuscles. This may be an important means of producing coelomic fluid by an ultrafiltration process and of transporting dissolved molecules between the two body-fluid systems. This view gains some support from the presence of similar blind capillaries on the nephridial blood vessels of *O. bicornis* and from the experimental evidence, based upon amino acid uptake, which is presented below. Studies such as those of KOECHLIN (1966), NAKAO (1974) and RUPPERT & SMITH (1988) suggest that efficient internal fluid transfer in polychaetes is often effected under pressure across the thin walls of capillaries, sometimes organised into plexuses. Such efficiency may be achieved in *Ophelia bicornis* by means of the inflatable blind capillaries described here.

There is, however, a more spectacular purpose to this system which is of mechanical nature and easily observed as it occurs within the prostomial coelom. The "injector organ", similar to that described by CLAPARÈDE (1870) in *Ophelia radiata*, is a structure formed from the two remaining segmental septa, which seals off the prostomial coelom of *Ophelia bicornis* from the main body coelom. Observation of active *O. bicornis* shows that the "injector organ" plays an important rôle in the increasing of prostomial coelomic fluid pressure, but it is a passive rôle. The walls of the organ do not contract to any appreciable extent in *O. bicornis* and therefore little, if any, of its contained fluid is squeezed into the anterior chamber. The passivity of the "injector organ" and the relative inelasticity of the prostomial cuticle combine to make the prostomial coelom not only a sealed chamber, but also a relatively inexpandable one.

b. The uptake of dissolved amino acids.

HARRIS (1991b,c) has indicated that *O. bicornis* probably supplements its diet to a very considerable extent by the uptake of dissolved organic material from the interstitial water and from the surfaces of the sand grains which are crammed into the gut during the feeding cycle. Investigations using radioactively-labelled glutamic acid have

Source : MNHN, Paris

shown that the radioactive marker accumulates to a greater extent in the anterior part of *O. bicornis* than elsewhere, as shown in Fig. 3. Autoradiographic investigation of thin sections of the anterior region shows that a considerable proportion of the labelled amino acid accumulates in the coelomic corpuscles of the sealed anterior chamber, Fig. 4.

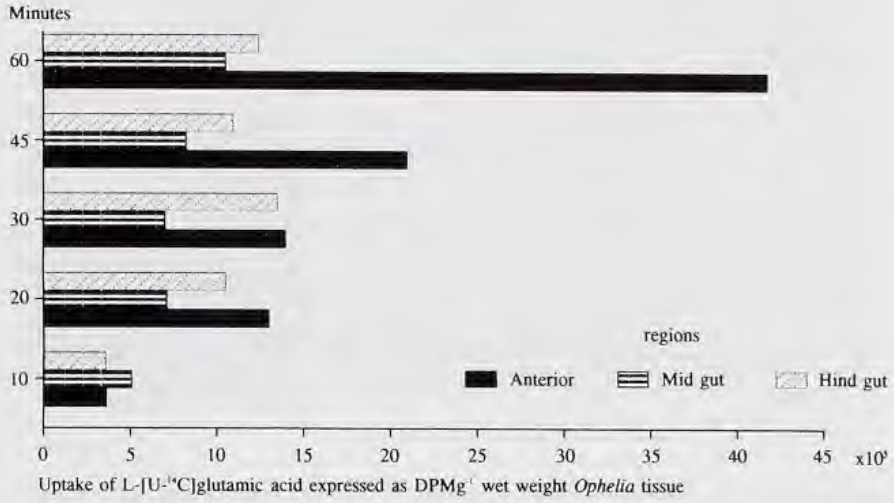



FIG. 3. — A bar chart showing typical uptake by *Ophelia bicornis* of radioactively-labelled glutamic acid over a sixty minute period. "Anterior" = the prostomium and buccal region, "Mid gut" = the central part of the body containing the absorptive part of the intestine, "Hind gut" = the rectum and pygidial papillae. DPM = disintegrations per minute in the scintillation counter.

## DISCUSSION

According to FAUVEL (1959) "L'appareil circulatoire des Sédentaires présente d'innombrables modifications en rapport avec la spécialisation des différentes régions du corps." Even within the context of such variety, the blood vascular system in the genus *Ophelia* is outstanding both in its structural modifications and in its functional relationships with the hydrostatic system and through both, with the behaviour and ecology of the worm. CLAPARÈDE (1870) described numerous blind vessels on the lateral vessels of *Ophelia radiata*: "Sur tout ce parcours le vaisseau dorsal et le vaisseau ventral sont mis en communication par une série d'anses. Le caractère le plus remarquable de cet appareil c'est que tous ces vaisseaux, surtout le dorsal et les anses, sont munis de centaines d'appendices aveugles, contractiles, dont le jeu alternatif de systole et de diastole est fort curieux à observer." He goes on to say that these structures are most numerous in the peripharyngeal region and are relatively rare within the prostomial coelom.

CLAPARÈDE (1870) described the "injector organ" as being of a tough, muscular nature and important to the generation of the prostomial rigidity which is so necessary for the penetration of sand. He said that this is accomplished by the contraction of the "appareil injecteur" by its own musculature, thus forcing into the enclosed prostomial coelom an additional volume of coelomic fluid, increasing the overall hydrostatic tension against the cuticle and so inducing a certain stiffness. In *O. bicornis* the "injector organ" seems to act only as the inelastic rear wall of the enclosed prostomial chamber.

At cardiac systole, the prostomial coelomic fluid is put under considerably increased pressure by the sudden and simultaneous inflation of the blind capillaries of the prostomial plexus. This pressure, developed against the inelastic cuticle, provides the necessary turgidity for the penetration of sand. At the same time, pressure is brought to bear on the anterior part of the pharynx which passes through the ventral wall of the "injector organ" and through the prostomial coelom and, due to the inflation of the plexus which lies external to the "injector organ", upon the posterior part of the pharynx also. This greatly facilitates the eversion, through the mouth, of the

Source : MNHN, Paris

voluminous pharynx tissues. It is probable that this pressure increase is supplemented by an increase in the volume of the pharyngeal coelomic fluid due to ultrafiltration through the greatly-expanded walls of the blind capillaries.

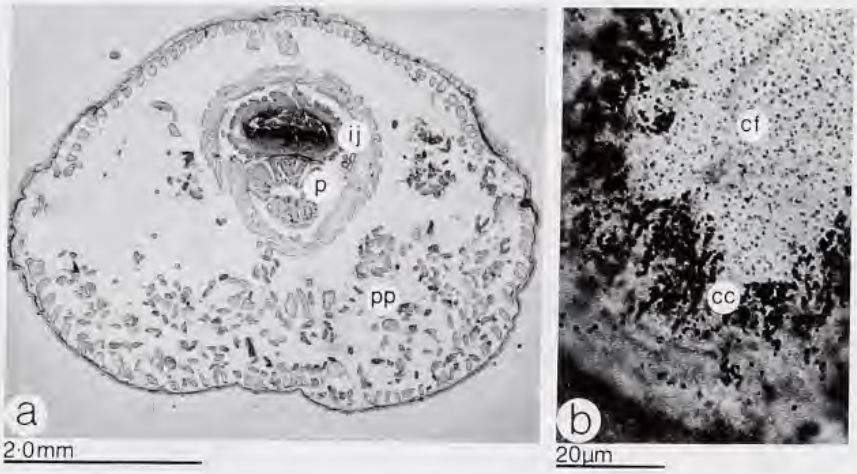



FIG. 4. — Autoradiographs of unstained sections of *Ophelia bicornis* after uptake of radioactive glutamic acid. a: a cross-section through the anterior pharyngeal region shows scattered concentrations of silver. b: part of the inner wall and coelom of the "injector organ" shows great concentration of silver in the coelomic corpuscles and scattered grains in the coelomic fluid. - cc, coelomic corpuscles. - cf, coelomic fluid. - ij, "injector organ". - p, pharynx. - pp, pharyngeal plexus.

HARRIS (1991a,c) described the typical habitat of *O. bicornis* in the Exe Estuary as being emersed for considerable periods, well — if not excessively — drained and meagre in potential food-sources and resistant to passage by a soft-bodied invertebrate. CHAPMAN and NEWELL (1947), having described the pressure which can be developed within the anterior coelom and proboscis of *Arenicola marina* state, suggested that this allows the worm to dig and to burrow effectively only when provided with thixotropic sand. It is not inappropriate to note, therefore, that the hydrostatic mechanism which is described here for *Ophelia bicornis* allows the worm to travel at all times with apparent ease through sand which is thixotropic for only relatively brief periods and dilatent for much longer ones.

The thinness of the gut-lining wall of the intestinal sinus of *O. bicornis* probably ensures the rapid transport of absorbed dissolved substances directly into the blood from the surfaces of the sand grains around which the walls of the gut wrap themselves in a totally-enveloping manner. This, coupled with the presence of a defaecation-enhancing device in the rectum (HARRIS, 1991b), gives an indication of the means which exist for efficient and constant nutrient uptake in this polychaete. Provision of a swift transport and storage mechanism, making use of an already-enhanced vascular system, would seem to be a logical ultimate development.

## CONCLUSION

The entire cycle of events may be summarised as follows:

a) *Ophelia bicornis* travels through highly resistant sand. Enhancement of the pressure within its prostomial hydrostatic skeleton by blood surges into expandable capillaries from a valved heart assists movement through the substrate.

b) Co-incidentally, the induced pressure system increases the efficiency of pharyngeal eversion and thus the intake of sand.

c) Nutrients absorbed from that sand are passed rapidly into the blood stream and efficiently flushed from the site of absorption to sites of temporary storage.

d) The same vascular apparatus permits rapid interchange of solutes between the blood and the coelomic fluid and its corpuscles which may act as one of the sites of food storage.

Source : MNHN, Paris

## ACKNOWLEDGEMENTS

I am grateful to Philip SHEARS for his unfailing and cheerful support in the laboratory and aquarium, to Margaret GRAPES for the benefit of her skill in handling the radio-isotope materials and to my colleague, Professor David NICHOLS for his continued interest, advice and constructive criticism.

## REFERENCES

ANSELL, A.D. & TRUEMAN, E.R., 1967. — Burrowing in *Mercenaria mercenaria* (L.) (Bivalvia, Veneridae). *J. exp. Biol.*, **46** : 105-115.

BROWN, R.S., 1938. — The anatomy of the polychaete *Ophelia cluthensis* McGuire, 1935. *Proc. R. Soc. Edinb.*, **58** : 135-160

CHAPMAN, G., 1950. — Of the movement of worms. *J. exp.Biol.*, **27** : 29-39

CHAPMAN, G., 1958. — The hydrostatic skeleton in the invertebrates. *Biol. Rev.*, **33** : 338-371

CHAPMAN, G. & Newell, G.E., 1947. — The role of the body fluid in relation to movement in soft-bodied invertebrates. I. The burrowing of *Arenicola*. *Proc. R. Soc., Ser.B*, **134** : 431-455

CLAPARÈDE, E., 1870. — Les annélides chétopodes du golfe de Naples, seconde partie. *Mém. Soc. Phys. Hist. nat. Genève*, **20** : 1-225.

DAWSON, R.M.C., ELLIOTT, D.C., ELLIOTT, W.H. & JONES, K.M., 1969. — *Data for Biochemical Research*. 2nd Edition, Oxford University Press, 654 p.

FAUVEL, P., 1959. — Organes des sens. Pages 95-119. *In* P.-P. GRASSÉ (éd), *Traité de Zoologie*. 5, Masson, Paris : 95-119.

HARRIS, T., 1991a. — The occurrence of *Ophelia bicornis* (Polychaeta) in and near the estuary of the River Exe, Devon. *J. mar. biol. Ass. U.K.*, **71** : 391-402.

HARRIS, T., 1991b. — The rectal organ of *Ophelia bicornis* Savigny (Polychaeta): a device for efficient defaecation. *Zool. J. Linn. Soc.*, **103** : 197-206.

HARRIS, T., 1991c. — Some aspects of the specific habitat requirements of *Ophelia bicornis* (Polychaeta). *J. mar. biol. Ass. U.K.*, **71** : 771-786.

KODAK Ltd., 1978. — Kodak materials for autoradiography. *Kodak Information Sheet* P- **64**(4): 1-14.

KOECHLIN, N., 1966. — Ultrastructure du plexus sanguin péri-oesophagien; ses relations avec la néphridie de *Sabella pavonina* Savigny. *C. r. hebd. Séanc. Acad. Sci., Paris, Sér. D*, **262** : 1266-1269.

NAKAO, T., 1974. — An electron microscope study of the circulatory system in *Nereis japonica*. *J. Morph.*, **144** : 217-235.

ROGERS, A.W., 1979. — *Practical autoradiography*. Amersham International, Amersham.

RUPPERT, E.E. & SMITH, P.R., 1988. — The functional organization of filtration nephridia. *Biol. Rev.*, **63** : 231-258.

TRUEMAN, E.R., 1966a. — The mechanism of burrowing in the polychaete worm, *Arenicola marina* (L.). *Biol. Bull.*, **131** : 369-377.

TRUEMAN, E.R., 1966b. — Observations on the burrowing of *Arenicola marina* (L.). *J. exp. Biol.*, **44** : 93-118.

TRUEMAN, E.R., 1968. — A comparative account of the burrowing process of species of *Mactra* and of other bivalves. *Proc. malac. Soc. Lond.*, **38** : 139-150.

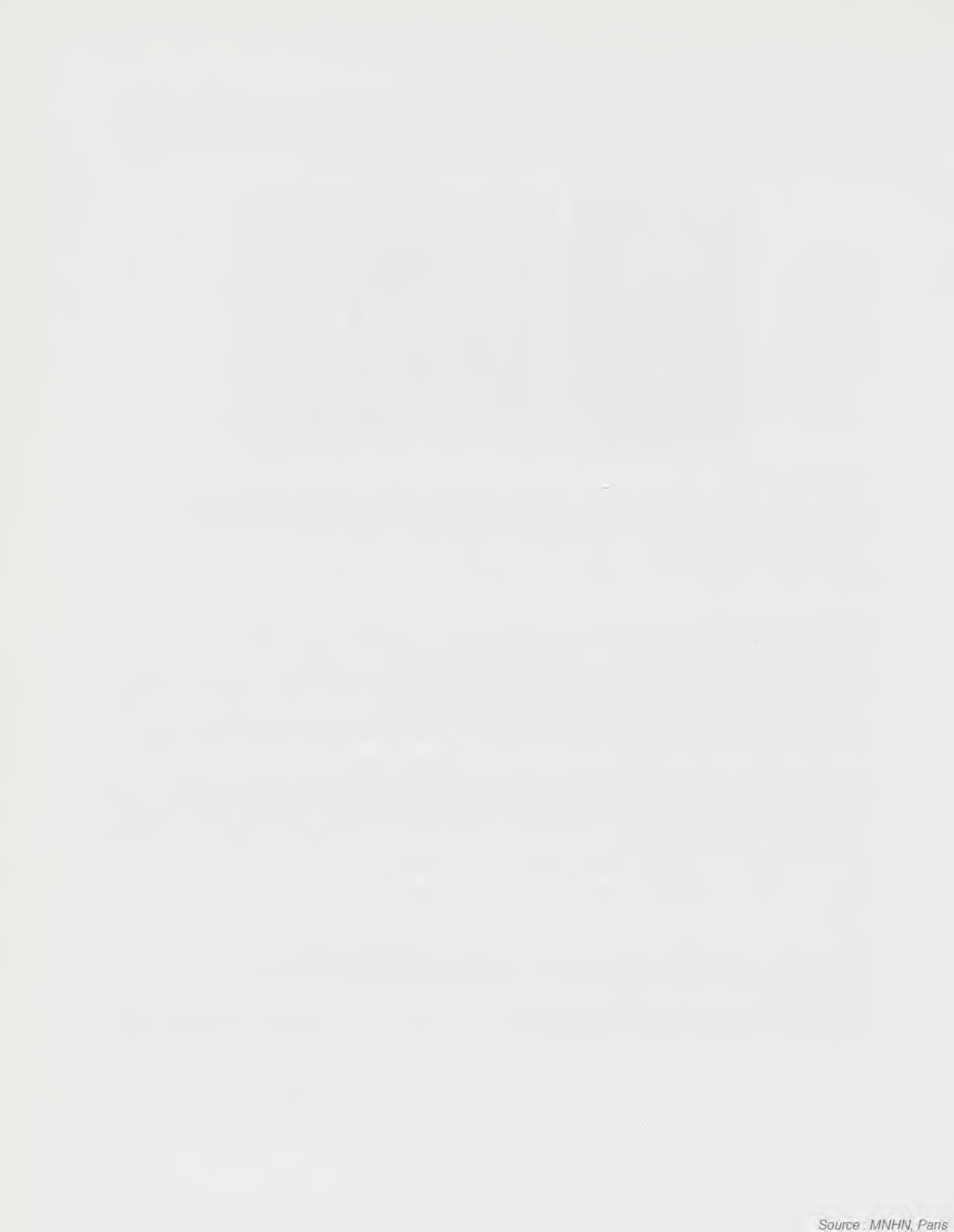
WELLS, G.P., 1944. — Mechanism of burrowing in *Arenicola marina* L. *Nature, Lond.*, **154** : 396.

WELLS, G.P., 1952. — The proboscis apparatus of *Arenicola*. *J. mar. biol. Ass. U.K.*, **31** : 1- 28.

WELLS, G.P., 1954. — The mechanism of proboscis movement in *Arenicola*. *Q. Jl Microsc. Sci.*, **95** : 251-270.

WELLS, G.P., 1961. — How lugworms move. Pages 209-233. *In:* J. A. RAMSAY & V.B. WIGGLESWORTH (eds), *The Cell and the Organism*. Cambridge University Press : 209-233.

Source : MNHN, Paris



Source : MNHN, Paris

# Feed-back regulation in *Platynereis dumerilii* Audouin & Milne-Edwards, 1833: a status review

*Dietrich K. HOFMANN*

Department of Zoology & Parasitology
Ruhr-University Bochum
D-4630 Bochum, Germany

ABSTRACT

In *Platynereis dumerilii*, gametogenesis and heteronereid transformations, as well as growth and regeneration of posterior parapodial segments, proceed under the endocrine control of presumeably a single hormone, which is produced by and released from the supraoesophageal ganglion. As the universal principle applying to all gonochoric, monotelic species in the family Nereidae investigated so far, this hormone controls postlarval development in a concentration-dependent manner. The juvenile growth-phase and the early stages of gametogenesis are determined by high hormone levels which, simultaneously, prevent precocious maturation and metamorphosis. Decreasing hormone levels correlate with gamete maturation, heteronereid metamorphosis and, on the other hand, with a loss of regenerative capacity. Neither oocyte differentiation beyond the critical stage nor spermiohistogenesis require additional hormone. The decline in hormone concentration in *P. dumerilii* is not based on a brain-autonomous control of hormone production and release but results from a more complex system of exogenous and endogenous factors acting on the cerebral ganglia. Severe amputation of segments in both maturing females and males was, but transection of the nerve cord was not the decisive factor for brain hormone activation. Removal of oocytes, injection of oocytes or of spermatogenic cells into juvenile hosts affect hormonal activity, and juvenile prostomia are inactivated when passaged in maturing males. The results are interpreted in terms of inactivation (or reactivation respectively) of brain hormone activity, caused by humoral feed-back emanating from coelomic cells, probably the germ cells. These findings are similar to but not identical with those concerning brain-body interactions in female *Nereis diversicolor* and *Perinereis cultrifera* . Isolation of a low molecular weight substance has been reported from the latter species, but the retroacting factor(s) in *Platynereis dumerilii* have not yet been analysed yet.

RÉSUMÉ

**Revue de la régulation en rétroaction chez *Platynereis dumerilii* Audouin & Milne-Edwards, 1833**

Chez *Platynereis dumerilii* la gamétogenèse et la métamorphose hétéronéréidienne, ainsi que la prolifération et la régénération de segments parapodiaux sont conditionnées par l'action d'une hormone élaborée par les ganglions cérébroïdes. Comme principe universel des espèces de Néréidiens à reproduction gonochorique et monotélique, le contrôle

HOFMANN, D.K., 1994. — Feed-back regulation in *Platynereis dumerilii* Audouin & Milne-Edwards, 1833: a status review. *In:* J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 65-72. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

hormonal du développement postlarvaire s'effectue en fonction de la concentration de l'hormone. La phase juvénile de croissance et le début de la gamétogenèse sont assurées par un taux hormonal élevé, qui, en même temps, inhibe la maturation et l'épitoquie précoce. Le progrès de la gamétogénèse, de la métamorphose et l'arrêt de la régénération postérieure se relient à une diminution progressive de l'activité endocrine. Par contre l'ovogenèse et la spermatogenèse, au delà d'une phase critique, sont achevées même sous des conditions anhormonales. La réduction caractéristique du taux de l'hormone au cours du cycle vital ne résulte pas du contrôle autonome de la synthèse et de la sécrétion par le cerveau lui-même mais ressort d'actions plus complexes de facteurs endogènes et exogènes sur les ganglions cérébroïdes. L'amputation d'un nombre substantiel de segments postérieurs altère le status endocrine des vers mâles et femelles proches de la maturité sexuelle. Néanmoins, la lésion de la chaîne nerveuse ventrale, due à l'opération, n'est évidemment pas la cause de la réactivation endocrine cérébrale que l'on constate. Cependant, l'enlèvement des ovocytes ou l'injection d'ovocytes submatures (ou de cellules spermatogénétiques) dans le coelome des vers juveniles, influence l'activité endocrine du contexte. En plus, des prostomiums prélevés sur des animaux juvéniles subissent une déactivation du cerveau au cours d'un passage dans le coelome des mâles s'approchant de la maturité. Ces effets sont considérés comme le résultat d'une rétroaction humorale sur l'activité endocrine cérébrale provenant vraisemblablement des produits génitaux. L'interdépendance humorale entre le corps et le cerveau constaté chez *Platynereis dumerilii* est comparable, mais n'est pas tout à fait identique à celle observée chez *Nereis diversicolor* et *Perinereis cultrifera*. Une substance provoquant l'arrêt de l'activité hormonale cérébrale a été isolée des ovocytes de la dernière espèce; par contre un facteur analogue n'a pas encore été identifié chez *P. dumerilii*.

## INTRODUCTION

Feed-back control means that a controlled system itself is acting back on its own control unit either to maintain or to alter a given physiological state. In the case of endocrine control of sexual maturation in nereid polychaetes, a feed-back phenomenon was first described by DURCHON (1952) in *Perinereis cultrifera*. He discovered that oocytes and associated coelomocytes taken from females approaching maturity ("ovocytes submatures", diameter ≥ 180 µm) and injected into immature males of the same species caused precocious gamete maturation and epitokous transformation. Since DURCHON (1948, 1952) had found out that maturation and epitoky are controlled by an inhibitory hormone originating from the prostomium, he concluded that the submature oocytes released a factor which down-regulated this inhibitory hormone, thus enhancing gamete maturation and heteronereid metamor-phosis. This was the first indication of possible interaction between the endocrine system and the maturing body.

All available data agree with the view that, as an universal principle in nereids, a single hormone, which is produced most probably in neurosecretory cells of the brain, controls postlarval development in a concentration dependant manner. It has been found to be neither species specific nor sex specific, and to work in species with and without epitokous reproductive form.

The present report considers currently available data on the regulation of endocrine activity in *Platynereis dumerilii*, one of the most thoroughly investigated nereid species. The following question is asked: is the brain hormone titer regulated by brain-autonomous control of production and release, or is it determined by a more complex system of exogenous and endogenous factors acting on the neurosecretory ganglia? In particular, I review results of investigations aimed at demonstrating feed-back phenomena during male and female gametogenesis, metamorphosis and regeneration of posterior segments. These findings are discussed and compared with studies bearing on feed-back control in *P. cultrifera* and on brain-body interaction in *Nereis diversicolor* (e.g. PORCHET & CARDON, 1976; PORCHET, 1984; GOLDING, 1987).

## DEVELOPMENT OF *PLATYNEREIS DUMERILII*

*P. dumerilii*, originally described from the Mediterranean and the french Atlantic coast, is a gonochoric, typically monotelic species, which develops a pelagic, epitokous reproductive form. Sex appears to be genetically controlled and the diploid complement of chromosomes was found to be 28 (HANSKE, 1989). The same diploid chromosome number was found also in the sibling species *P. massiliensis* and *P. megalops* (D. JÖRG, Univ. Mainz, pers. comm.). In neither sex are typical gonads present, gametogenesis proceeds in the coelomic fluid. Recently, HANSKE (1989) detected paired, segmental sites at dorsolateral positions, from which small clusters of spermatogonia appear to be proliferated and released into the coelom (but see the findings in *Nereis grubei* by REISH, 1954). Metamorphosis into the reproductive form parallels the final stages of gamete development; the pelagic heteronereis then broadcasts the fully mature eggs and sperm during pheromone controlled nuptial dances

Source : MNHN, Paris

(ZEEK *et al.*, 1988 for review). There is no brood protection; early phases of development, including trochophore and metatrochophore stages, are pelagic. Nectochaeta larvae later start settling and forming tubes on the substratum from secretions of parapodial glands. In laboratory cultures maintained by now standard methods (HAUENSCHILD, 1951), development from fertilized egg to the heteronereis stage is variable and takes from 3 to 12 months with a small proportion of "stragglers" taking up to 18 months (HAUENSCHILD, 1966). Of a total of 635 males 65% reached maturity within 4-8 months (HANSKE, 1989); the same author recorded a similar life-span for females. With its very short life-cycle, correlated with rapid growth and fast regeneration, *P. dumerilii* differs considerably from *P. cultrifera* and *Nereis diversicolor* which require 2-3 years to reach the reproductive status in the field.

## ENDOCRINE CONTROL OF POSTLARVAL DEVELOPMENT

Results of the pioneer work by DURCHON (1948, 1952), performed first on male *Nereis irrorata* and *Perinereis cultrifera*, suggested that spermatogenesis and epitokous metamorphosis are controlled by an inhibitory, endocrine factor formed within the prostomium. Using female worms, HAUENSCHILD (1956, 1965, 1966) conducted prostomium amputation experiments on laboratory reared *P. dumerilii*, focussing on gametogenesis, metamorphosis and caudal regeneration. His results largely confirmed DURCHON's observations, but moreover, provided a much more detailed hypothesis of the hormonal control mechanism in this species. He concluded that a single prostomial hormone is responsible for the control of both gametic and somatic development, acting in a concentration dependent manner. The juvenile growth phase and proliferation of germ cells require a high titer of hormone, which inhibits late stages of gametogenesis and epitokous transformations. When oocytes reach diameters of 80-100 µm, a photoperiodically triggered decrease of hormone concentration initiates a new phase of oocyte growth and differentiation, stops the addition of new segments, quenches posterior regeneration, and allows then metamorphosis of somatic tissues. Once the level approaches zero, development of heteronereid swimming setae is completed and oocytes undergo final maturation. The heteronereis then aquires the competence to respond to sex pheromones, i.e. to perform nuptial dances and to shed the gametes soon after it begins to swim. Since absolute hormone concentrations could not be measured, HAUENSCHILD (1965) used arbitrary units and suggested, but did not indicate in his Fig. 19, a logarithmic scale. DURCHON & PORCHET (1971), PORCHET (1973), and SCHROEDER *et al.* (1977) arrived at similar conclusions when studying developing individuals of several species of nereids, despite the fact that the former authors were using an entirely different organ-culture system to assay the hormonal activity of homogenized prostomia (see BERTOUT, 1984 for details of the *N. diversicolor* spermatogenesis assay).

The major drawback of the work discussed herein is that the precise site of production and release of the hormone, its molecular structure, its rate of synthesis and secretion, and its absolute concentrations are not yet known. We must use live prostomia, or homogenates (fresh or lyophilized) as a source of the active compound, and we have to deduce or to determine indirectly relative values of hormone activity (or concentrations respectively) from biological assays based on morphogenic or cytomorphologic criteria.

All recent evidence confirms the view that the hormone concentration in *Platynereis dumerilii* is maximal in juvenile animals and decreases to zero in the heteronereid, and a high level of activity is required to sustain segment formation, to support the proliferation of oogonia and spermatogonia, and to suppress premature maturation and epitoky (HOFMANN, 1975, 1976; SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984; MEISEL, 1990). It has been confirmed that growth and regeneration capacity decrease and somatic metamorphosis starts when the hormone level is lowered. However is has become a matter of dispute whether all successive developmental events in somatic tissues and germ cells are directly controlled by specific levels of hormonal activity. HAUENSCHILD (1966) found that oocytes,which had a critical diameter of about 100 µm, completed a morphologically normal oogenesis after the prostomium had been removed. No further hormone supply was required at that stage. On the other hand, implantation of one or two prostomia from juveniles into female recipients with oocytes of diameters larger than 100 µm significantly prolonged the time of survival, but retarded and disturbed both oogenesis and metamorphosis when compared to either decapitated worms or controls. Though oocyte development beyond the critical stage can proceed without continued hormone secretion, the maturing oocytes are still sensitive to altered endocrine conditions (HOFMANN, 1975).

The same type of experiments led to different results when performed on males. Prostomial removal from juveniles caused defective development at the end of which the worm fragments were still lacking major heteronereid characters and did not contain any gametes. Individuals with some small clusters of spermatogonia in the coelom (early spermatogonia cluster I phase) showed a dual response. Whereas metamorphosis was defective in

Source : MNHN, Paris

all cases, the course of spermatogenesis was morphologically normal. None of the stages was omitted but the entire sequence was accelerated ; it took only 12.5 days on the average instead of one to several months to produce mature spermatozoa. If, however, worms were decapitated at the end of the first mitotic proliferation phase (late spermatogonia cluster I phase), not only spermatogenesis but also metamorphosis was accelerated. At this stage 93% of the experimental worms developed normal heteronereid characters (MEISEL, 1990).

Implantation of one to three prostomia from juvenile donors into developing males, from the advanced spermatogonia cluster stage onward, left spermatogenesis unaffected. Differentiation of sperm proceeded at about the normal rate. This is in obvious contrast to the findings in females. On the other hand, heteronereid transformation was strongly affected and disordered by this manipulation of the hormone level, as in the corresponding experiments on female *P. dumerilii* (SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984).

Gamete development in both sexes and metamorphic events appear to be strictly coordinated in ontogenesis, but to be experimentally dissociable. Spermatogenesis turns out to be considerably less sensitive to the alteration of endocrine conditions than oogenesis. It is remarkable that development of heteronereid characters can be seriously delayed and disturbed by manipulating the endocrine status even very late in gametogenesis. The sibling species *P. massiliensis*, although morphologically indistinguishable from *P. dumerilii*, has an entirely different, benthic mode of reproduction. These proterandric hermaphrodites do not metamorphose; they deposit, fertilize, and brood the eggs within their tubes. Posterior regeneration was shown to decrease drastically in the absence of the prostomium (CASANOVA, 1955), but no unequivocal proof of brain hormone control of either spermatogenesis or oogenesis could be developed (HAUENSCHILD, 1970; LÜCHT, 1987 for review).

## FACTORS AFFECTING THE ENDOCRINE ACTIVITY OF THE BRAIN

### ENVIRONMENTAL FACTORS

HAUENSCHILD (1966) demonstrated photoperodic control of swarming periodicity in *P. dumerilii* and has further shown maturation and epitoky to be hormonally governed. He therefore postulated that the synodic or experimentally modified light-dark regime acts via the neuroendocrine pathway. However, no detailed study on light-to-hormone signal conversion is available to prove this hypothesis.

Temperature has been reported to affect hormone gamete-interaction in *N. diversicolor* (DURCHON & PORCHET, 1971), but the influence of temperature on development and endocrine activity has not been studied in *P. dumerilii*.

## REGENERATION OF POSTERIOR SEGMENTS

The number of setigers regenerated following amputation of the posterior end is positively correlated with the number of segments removed. As mentioned earlier, at a given level of transection, the number of segments regenerated decreases concomitantly with the progress of gamete maturation and metamorphosis (HAUENSCHILD, 1966; HOFMANN, 1966; SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984). HAUENSCHILD (1966) also noticed that in maturing females amputation of a significant number of posterior segments led not only to regeneration but also to retardation of sexual development and to delayed metamorphosis. These results suggest that hormone production has been stimulated, possibly mediated by the injury of the ventral nerve cord (see HOFMANN, 1966 for discussion of earlier work). More detailed investigations in female *P. dumerilii* showed that maturation was delayed and significant regeneration occurred only when about 50 of approximately 70 parapodial segments were removed. Furthermore, the size of the regenerate and the delay in reaching the heteronereis stage decreased as individuals of more advanced stages of sexual development were assayed (HOFMANN, 1975).

In males, the number of segments regenerated and the delay in heteronereid metamorphosis are likewise correlated with the number of segments amputated and with the stage of sexual development. However, spermatogenesis continued unaffected when males from the late spermatogonial stage onward were assayed. In such cases we observed males deprived of all but 20 segments which showed posterior regeneration and significant delay of metamorphosis, but in which spermatogenesis proceeded independently. They contained mature spermatozoa a full three weeks before reaching the heteronereis stage.

The hypothesis that the site of nerve cord lesion causes a position-dependent increase in hormone production and thus determines the course of regeneration and maturation was tested. In males and females at selected stages of development, the ventral nerve cord was excised from segments 20 and 21 (or the circumoesophageal connectives

Source : MNHN, Paris

deleted) prior to amputation of the posterior end behind segment 40 (HOFMANN, 1966, 1975; SCHIEDGES, 1981). The results did not support the assumption that nerve cord injury activates hormone secretion and thus enhances posterior regeneration accordingly. Therefore, stimulation of the neurosecretory cells via the nervous system does not appear to be the decisive control mechanism. There must be other components modulating brain hormone activity by stimulating its production or by temporarily preventing its decrease. Candidates are the developing gametes, the somatic coelomocytes interspersed with the gametes, and various somatic tissues.

## FEED-BACK ACTIVITY OF GAMETES AND COELOMOCYTES

When deprived of all but 20 segments, female *P. dumerilii* with oocytes measuring 130-150 µm in diameter regenerated up to 12 segments and survived up to 25 days, whereas those cut behind segment 40 did not form regenerates but transformed into heteronereids within one week, as did the controls. Amputation of about 2/3 of the animals parapodial segments means that the hormone "source" has to serve thereafter only a much smaller part of its "sink". Even at a given, constant production of the factor, a higher concentration may result in the much smaller body and could account for enhanced regeneration and retarded heteronereid development. If one bears in mind that some cells of the "sink" acquire the ability to feed back on and to inhibit the hormone producing cells, cutting off segments involves not only a decrease of the "sink" volume, but also a reduction of the mass of cells feeding back on the hormone source.

DURCHON (1952) suggested that a coelomic factor associated with the oocytes and eleocytes of submature *P. cultrifera* reduced the endocrine activity of the brain in immature recipients injected with gametocytes and coelomocytes.

Several lines of evidence indicate that down-regulating factor(s) exist in *P. dumerilii* as and are major components of developmental control (HOFMANN, 1975; SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984; MEISEL, 1990). In these investigations, the number of segments regenerated by males and females at selected stages of development, the time period required to form the heteronereis, or the survival time, were used to determine such effects.

## REMOVAL AND INJECTION OF COELOMIC CONTENTS

Removal of oocytes and coelomocytes by stripping following caudal amputation led to enhanced regeneration and to significantly delayed metamorphosis at stages in which regeneration had normally ceased (HOFMANN, 1975). When intact juvenile worms were deprived of all but 40 segments and were injected with the coelomic contents of females with oocytes ranging from 100 to 180 µm in diameter, effects on the recipient's development were observed only when 100 to 120 µm oocytes were injected. Seven out of 15 juvenile recipients started to regenerate but then stopped and transformed into heteronereis within 11 to 17 days, whereas controls took one to several months (HOFMANN, 1975).

Stripping of gonia from males was much more difficult and could not be done quantitatively. The experimentals were apparently affected by the manipulation and did not develop well. This will not be considered further (SCHIEDGES, 1981). Injection of mature spermatozoa and coelomocytes into very young females (oocyte cluster stage) caused accelerated oocyte growth and metamorphosis, and significantly reduced the regeneration of posterior segments. Quite unexpectedly, males at the initial stage of gametogenesis did not respond to sperm injection. On the other hand, juvenile worms, when injected with gonia from spermatocyte/tetrad or tetrad stage donors, metamorphosed much faster than the controls, *i.e.* in only about 62 % of the time. However regeneration was clearly reduced only when the colomic contents of tetrad stage donors was transferred (SCHIEDGES, 1981).

These observations are compatible with the hypothesis that factors, probably stage specific, are associated with gametes and coelomocytes, which influence development by altering the endocrine activity of the brain. Under these premises stripping of the oocytes means removal of the feed-back factor and results in hormone production and, consequently, in enhanced regeneration and delayed metamorphosis. On the other hand, injection of differentiating gametes and coelomocytes adds such factors which then suppress hormone production in the immature host. This would account for their limited regeneration and accelerated epitokous development and maturation.

Source : MNHN, Paris

## PROSTOMIUM TRANSFER EXPERIMENTS

Additional evidence for the existence of coelomic factors which feed back on hormone production has been provided by prostomium transfer assays. HAUENSCHILD (1966) found that prostomia taken from maturing females and implanted into decapitated fragments of younger females, exhibited a stronger maturation inhibiting and regeneration promoting activity than they would have *in situ*. He assumed that the different "environment" in the younger recipients had somehow stimulated the activity of the implant. SCHIEDGES (1981) systematically tested the properties of prostomia taken from males at different spermatogenetic stages and transferred to juvenile, decapitated hosts. She noticed that prostomia excised from worms at the spermatocyte cluster stage, the spermatocyte/tetrad stage and at the tetrad stage could be assigned a higher endocrine activity than when tested *in situ*, thus confirming and extending HAUENSCHILD's result.

SCHIEDGES (1981) provided further support through very elegant prostomium passaging experiments performed on *P. dumerilii*. Prostomia excised from immature donors were implanted into male intermediate hosts at different stages of spermatogenesis and were left there for one week. Then the prostomia were excised again and implanted into definitive, immature, decerebrate 40 segment host fragments.

In individuals receiving prostomia which had been passaged in intermediate hosts ranging from the juvenile state to the spermatocyte /tetrad stage there was a slight decline in both numbers of segments regenerated and in survival time, compared to the controls. However a significant decrease occured only in those receiving prostomia which had been passaged through intermediate hosts at the tetrad or sperm stage. This proved that the secretory activity of prostomia is negatively affected when exposed to the coelomic "environment" of maturing males. This influence appears to be stage dependent and to be strongest during the last two spermatogenic stages. Isolation and characterization of factors which exert negative feed-back on endocrine activity and which do not appear to be sex specific, has not yet been attempted in *P. dumerilii*.

## FEED-BACK CONTROL OF BRAIN HORMONE ACTIVITY IN OTHER NEREID POLYCHAETES

Extending DURCHON's (1952) earlier work, PORCHET (1967), PORCHET & DURCHON (1968), and PORCHET & CARDON (1972, 1976) studied the effect of maturing oocytes ("ovocytes submatures", diameter $\geq$ 180 µm) injected with their adhering coelomocytes into recipient male and female worms at different stages of development in *P. cultrifera*. In this species, which takes three years to reach sexual maturity, oocyte transfer turned out to cause long-term effects, observed only after many weeks or even months. Injection of submature oocytes into juvenile hosts led to precocious gametogenesis: 93 % of the males produced sperm and also transformed into heteronereids within 110 days. Surprisingly, female recipients underwent only abortive, although accelerated oogenesis but did not metamorphose, in contrast to the findings in *P. dumerili* (HOFMANN, 1975; SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984). Injection of coelomic contents was also found to affect posterior regeneration, *i.e.* the number of segments regenerated was negatively correlated with the size of the injected oocytes. After carrying submature oocytes for 50 days, initially juvenile recipients failed to regenerate any segments within a period of 20 days, though controls regenerated an average of 14 segments.

PORCHET & CARDON (1972, 1976) showed that the precocious gametogenesis, epitoky, and inhibition of regeneration, which followed injection of submature oocytes, was not a response to the injection. They demonstrated that the effect is based on a chemical factor, the action of which could only be interpreted in terms of down-regulation of brain hormone activity in the recipient. In separate assays, they examined the biological effect of oocytes, coelomocytes, coelomic fluid, and of extracts of somatic tissues on host animals. They found that the factor causing brain hormone inactivation is associated exclusively with the oocyte fraction. PORCHET & CARDON (1976) purified the factor from an aqueous ethanolic oocyte extract. The compound appears to be a low molecular weight substance which is dialysable, heat labile, resistant to proteolytic enzyme action, and ninhydrine positive. It does not seem to be a peptide, but has been suspected to be a glycoprotein. The feed-back substance is obviously different from the two peptides, $B_1$ and $B_2$, also isolated from the coelomic fluid of *P. cultrifera*, which stimulate the final phase of oocyte differentiation (PORCHET *et al.*, 1979).

GOLDING (1967, 1983, 1985, 1987) provided a large body of evidence for humoral brain-body interaction in *N. diversicolor* which corroborates many of the findings and conclusions reported above. *N. diversicolor* reaches maturity in the second or third year of life. It does not develop a pelagic heteronereis but shows an atokous, benthic reproductive form. Gamete maturation is accompanied by the progressive loss of capacity to proliferate and

Source : MNHN, Paris

regenerate posterior segments. As in the other nereid species considered here, decreasing brain hormone levels account for this developmental pattern.

Prostomium passaging experiments involving prostomia from female donors at various stages of oogenesis and using both immature and maturing intermediate hosts, demonstrated that the endocrine activity can be influenced in either direction. Prostomia from maturing donors, known to exhibit only reduced regeneration promoting activity, were apparently reactivated when subjected to repeated intracoelomic conditioning in immature intermediate hosts. On the other hand, deactivation of prostomia was observed after passaging for a prolonged time period in maturing hosts. Deactivation was readily achieved in prostomia excised from donors at later oogenetic stages, but failed to occur in some of those taken from juvenile worms. Furthermore, injection of submature oocytes into immature *N. diversicolor* had a long-term negative effect on regeneration, provided that the injected oocytes did not degenerate. However final oocyte maturation and spawning was not normally observed in these individuals. Thus, submature oocytes can be assigned a brain hormone deactivating influence in *N. diversicolor*, too.

The results of the prostomium passaging experiments can be interpreted, as proposed in *Platynereis dumerilii*, in terms of inhibition and activation of neuroendocrine activity of the respective prostomia, though no information is available on the regulatory mechanism. Although humoral retroaction on brain hormone activity has been demonstrated also in male *P. dumerilii* (SCHIEDGES, 1981; HOFMANN & SCHIEDGES, 1984), no corresponding investigations seem to have been done on male *P. cultrifera* or *Nereis diversicolor*. Feed-back control in oogenesis of *Cirratulus cirratus* (OLIVE, 1973) and in spermatogenesis of *Arenicola marina* (HOWIE, 1984 for review) are well-known examples of retroaction in gametogenesis of polychaetes. They are not related, however, to the system of gamete-brain-soma interaction discussed here for members of the family Nereidae.

## ACKNOWLEDGEMENTS

I am indebted to J. FLECK for reading and commenting upon the manuscript. The valuable advice of an anonymous referee and of D.J. REISH is gratefully acknowledged.

## REFERENCES

BERTOUT, M., 1984. — Spermatogenesis in *Nereis* as a model for the endocrine control of meiosis. *Fortschr. Zool.*, **29** : 115-122.

CASANOVA, R., 1955. — Influence du prostomium sur la régénération caudale de *Platynereis massiliensis*. *C.R. hebd. Acad. Sci.* (Paris), **241** : 1814-1816.

DURCHON, M., 1948. — Épitoquie expérimentale chez deux polychètes : *Perinereis cultrifera* et *Nereis irrorata*. *C. R. hebd. Acad. Sci.* (Paris), **227** : 157-158.

DURCHON, M., 1952. — Recherches expérimentales sur deux aspects de la reproduction chez les Annélides Polychètes: l'épitoquie et la stolonisation. *Ann. Sc. Nat. (Zool. Biol. anim.)* Sér. XI, **14** : 119-206.

DURCHON, M. & M. PORCHET, 1971. — Premières données quantitatives sur l'activité endocrine du cerveau des Néréidiens au cours de leur cycle vital. *Gen. comp. Endrocinol.*, **16** : 555-565.

GOLDING, D. W., 1967. — Endocrinology, regeneration and maturation in *Nereis*. *Biol. Bull.* (Woods Hole), **133** : 567-577.

GOLDING, D. W. , 1983. — Endocrine programmed development and reproduction in *Nereis*. *Gen. Comp. Endocrinol.*, **52** : 456-466.

GOLDING, D. W., 1985. — Brain-body interactions in *Nereis*. Reactivation of the cerebral neuroendocrine system by endocrine manipulation. *Int. J. Invert. Reprod. & Devel.*, **8** : 51-59.

GOLDING, D. W., 1987. — Brain-body interactions in *Nereis*. Deactivation of the cerebral neuroendocrine system by ganglion transplantation. *Int. J. Invert. Reprod. & Devel.*, **12** : 281-294.

HANSKE, M., 1989. — *Gametogenese eines monotelischen Anneliden: Beobachtungen zur Gonienherkunft, zum Verlauf und zur Feinstruktur der Spermatogenese bei* Platynereis dumerilii *(Annelida: Polychaeta)*. Doctoral Dissertation, Ruhr-University, Bochum, 104 pp.

Source : MNHN, Paris

HAUENSCHILD, C., 1951. — Nachweis der sog. atoken Geschlechtsform des Polychaeten *Platynereis dumerilii* (Aud. & Milne-Edw.) als eigene Art auf Grund von Zuchtversuchen. *Zool. Jb. Physiol.*, **63** : 107-128.

HAUENSCHILD, C., 1956. — Hormonale Hemmung der Geschlechtsreife und Metamorphose bei dem Polychaeten *Platynereis dumerilii*. *Z. Naturf.*, **11b** : 610-611.

HAUENSCHILD, C., 1965. — Hormone bei Nereiden und anderen niederen Wirbellosen. *Zool. Jb. Physiol.*, **71** : 511-544.

HAUENSCHILD, C., 1966. — Der hormonelle Einfluß des Gehirns auf die sexuelle Entwicklung bei dem Polychaeten *Platynereis dumerilii*. *Gen. Comp. Endocrinol.*, **6** : 26-73.

HAUENSCHILD, C., 1970. — Beziehungen zwischen Gehirnhormon und Geschlechtsdifferenzierung beidem proterandrischen Polychaeten *Platynereis massiliensis*. *Zool. Anz., Suppl. Bd.*, **33** : 249-253.

HOFMANN, D.K., 1966. — Untersuchungen zur Regeneration des Hinterendes bei *Platynereis dumerilii* (Audouin & Milne-Edwards) (Annelida, Polychaeta). *Zool. Jb. Physiol.*, **72** : 374-430.

HOFMANN, D.K., 1975. — Analysis of the relationship between regeneration, maturation and endocrine system in the polychaete *Platynereis dumerilii*. *Verh. Dtsch. Zool. Ges. Bochum 1974*, Gustav Fischer Verlag, Stuttgart: 314-319.

HOFMANN, D.K., 1976. — Regeneration and endocrinology in the polychaete *Platynereis dumerilii*. *Wilhelm Roux' Arch. Devel. Biol.*, **180** : 47-71.

HOFMANN, D.K. & I. SCHIEDGES, 1984. — Brain hormone levels and feed-back regulation during gametogenesis, metamorphosis and regeneration in *Platynereis dumerilii* - An experimental approach. *Fortschr. Zool.*, **29** : 73-79.

HOWIE, D.I.D., 1984. — The reproductive biology of the lugworm, *Arenicola marina*. *Fortschr. Zool.*, **29** : 247-263.

LÜCHT, J., 1987. — *Experimentelle und morphologische Untersuchungen zur Geschlechtsreifung und Fortpflanzung bei dem proterandrischen Polychaeten* Platynereis massiliensis. Doctoral Dissertation, Freie Universität, Berlin, 126 pp.

MEISEL, J., 1990. — *Zur Hormona Abhängigkeit der Spermatogenese bei* Platynereis dumerilii: *Licht-und elektronen-mikroskopische Befunde sowie experimentelle Untersuchungen* in vivo *und* in vitro. Doctoral Dissertation, Ruhr-University Bochum, 166 pp.

OLIVE, P.J.W., 1973. — The regulation of ovary function in *Cirratulus cirratus* (Polychaeta). *Gen. Comp. Endocinol.*, **20** : 1-15.

PORCHET, M., 1967. — Rôle des ovocytes submatures dans l'arrêt de l'inhibition cérébrale chez *Perinereis cultrifera* Grube. *C. R. hebd. Acad, Sci.* (Paris), **265** (D) : 1394-1396.

PORCHET, M., 1972. — Variation de l'activité endocrine des cerveaux en fonction de l'espèce, du sexe et du cycle vital chez quelque Néréidiens (Annélides Polychètes). *Gen. Comp. Endocrinol.*, **18** : 276-283.

PORCHET, M., 1984. — Biochemistry of oocyte differentiation in nereids. *Fortschr. Zool.*, **29** : 207-225.

PORCHET, M. & C. CARDON, 1972. — Régulation de l'activité endocrine cérébrale chez les Nereidae (Annélides Polychètes). *C. R. hebd. Acad. Sci.* (Paris), **275** (D) : 2375-2378.

PORCHET, M. & C. CARDON, 1976. — The inhibitory feed-back mechanism coming from oocytes and acting on brain endocrine activity in *Nereis* ( Polychaetes, Annelids). *Gen. Comp. Endocrinol.*, **30** : 378-390 .

PORCHET, M. & M. DURCHON, 1968. — Influence de la maturité génitale sur la régénération postérieure, chez *Perinereis cultrifera* Grube (Annélide Polychète). *C. R. hebd. Acad. Sci.* (Paris), **267** (D) : 94-196.

PORCHET, M., DHAINAUT, A. & E. PORCHET-HENNERE, 1979. — Evidence of coelomic substances inducing genital maturation in *Perinereis cultrifera*. *Wilhelm Roux' Arch. Devel. Biol.*, **186** : 129-137.

REISH, D.J., 1954. — The life history and ecology of the polychaetous annelid *Nereis grubei* (Kinberg). *Occ. Pap. Allan Hancock Found.*, **14** : 1-75.

SCHIEDGES, I., 1981. — *Spermatogenese, Metamorphose, Regeneration und deren Beziehung zum neuroendokrinen System bei* Platynereis dumerilii. Doctoral Dissertation, University of Cologne, 94 pp.

SCHROEDER, P.C., E. HOFMANN & K. WALLACE, 1977. — Posterior regeneration and the endocrine control of postlarval development in *Nereis grubei* (Kinberg). *In* D.J. REISH, & K. FAUCHALD (eds.), *Olga Hartman Memorial Volume*. Special Publ. Allan Hancock Foundation, Los Angeles, Calif. : 391-405.

ZEECK, E., HARDEGE, J., BARTELS-HARDEGE, H & G. WESSELMANN, 1988. — Sex pheromone in a marine polychaete: Determination of the chemical structure. *J. exp. Zool.*, **246** : 285 -292.

Source : MNHN, Paris

# Bioaccumulation du fer dans le corps cardiaque de *Raricirrus beryli* Petersen & George (Polychaeta, Ctenodrilidae)

*Jean VOVELLE*, Mary E . PETERSEN**, Michèle GRASSET * & Patricia BEAUNIER****

*Laboratoire d'Histologie et Cytologie des Invertébrés Marins
Université P. et M. Curie
12, rue Cuvier, F-75005 Paris, France
**Zoological Museum, University of Copenhagen
Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark
***Service de Microscopie électronique GRMP
Université P. et M. Curie
6, rue Cuvier, F-75005 Paris, France

RÉSUMÉ

*Raricirrus beryli*, localement abondant dans les champs pétrolifères de la mer du Nord septentrionale, est reconnu comme une espèce indicatrice pour les sédiments pollués par les hydrocarbures. Le matériel provient de deux récoltes : à proximité nord de la Beryl Platform (mai 1982) et à 200 m nord du premier site (mai 1985). Sa conservation a permis d'entreprendre une étude microanalytique (au moyen de la microsonde en dispersion de longueur d'onde, du microanalyseur ionique et de la microsonde en dispersion d'énergie) et d'obtenir des indications sur sa structure cytologique. L'organe étudié est le corps cardiaque, dont le rôle possible de détoxification peut se traduire par des différences entre les spécimens des deux récoltes. Les éléments détectés par la microanalyse sont surtout le fer, et en quantités moindres du calcium, soufre, phosphore et aluminium. Les autres éléments repérables sont le magnésium, le chlore, des traces de cuivre, de vanadium et de fluor ; zinc et silice sont absents. Le fer a été identifié à l'échelle ultrastructurale sous la forme de particules intracytoplasmiques de ferritine, concentrées souvent dans des inclusions délimitées par une membrane ou intégrées à des granules sphérulaires. La différence entre les deux récoltes se manifeste dans la teneur en fer, trois fois plus forte dans les spécimens à proximité de la plateforme. Chez quelques uns d'entre eux, le fer apparaît à l'échelle ultrastructurale comme un feutrage d'aiguilles entourant certaines sphérules. Cette surcharge complique la fonction hématopoiétique supposée du corps cardiaque, on suggère qu'elle joue un rôle dans la détoxification.

ABSTRACT

**Iron bioaccumulation in the heart body of *Raricirrus beryli* Petersen & George (Polychaeta, Ctenodrilidae)**

---

VOVELLE, J., PETERSEN, M.E., GRASSET, M. & P. BEAUNIER, 1994.— Bioaccumulation du fer dans le corps cardiaque de *Raricirrus beryli* Petersen & George (Polychaeta, Ctenodrilidae). *In:* J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 73-80. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

*Raricirrus beryli*, which is abundant in the oilfields of the northern North Sea, has been recognised as an indicator species for hydrocarbon-polluted sediments. The material came from two different sites in the North Sea: one just north of the Beryl platform May 1982), the other 200 meters north or the platform (May 1985). A microanalytical study was carried out using a wavelength X-ray spectrometry microprobe, an ion microanalyser, and an energy dispersive spectrometry microprobe. The cytological structure of the dorsal heart body was studied from sections embedded in araldite. The elements detected under microanalysis were mainly iron and small amounts of calcium, sulfur, phosphorus, aluminium, magnesium, chlorine, copper, vanadium and fluorine. Neither zinc nor silica were detected. Iron was identified as a form of intracytoplasmic ferritin particles which were concentrated in membrane-bound inclusions or integrated with spherular granules. The main difference between the two sites was in the amount of iron, which was three times greater in specimens close to the platform as in those from 200 meters. Iron was detected at the ultrastructural level in the form of needles surrounding some of the spherules from some specimens collected near the platform. This overload of iron is not in keeping with the supposed haematopoietic function of the heart body, it is hypothezed that it plays a part in the detoxification process.

## INTRODUCTION

L'animal retenu pour cette étude, *Raricirrus beryli*, a été décrit en 1991 (PETERSEN & GEORGE, 1991) et reconnu comme une nouvelle espèce de polychète indicatrice pour les sédiments pollués par les hydrocarbures (MOORE, 1991). Les échantillons qui ont permis notre recherche ont été recueillis dans deux sites différents : l'un à proximité de la plateforme pétrolière Beryl dans la mer du Nord, l'autre 200 m plus loin. Même si l'écart de temps qui sépare les deux récoltes relativise la rigueur de nos conclusions, la différence d'aspect des corps cardiaques des animaux dans les deux récoltes impose l'hypothèse de leur intervention dans un processus de détoxification. Leur conservation ne permettait pas d'envisager une étude cytologique fine, mais du moins l'appréciation de différences significatives dans leur composition élémentaire, par les méthodes de la microanalyse à l'échelle structurale et ultrastructurale.

L'interprétation du corps cardiaque présent chez cinq familles de Polychètes a fait l'objet de nombreux travaux. Si l'on admet maintenant son homologie avec le tissu chloragogène "extravasal" qu'on trouve dans d'autres familles, on sait aussi que ce dernier a pu être décrit comme un rein d'accumulation avant qu'on examine son rôle dans l'hématopoièse. La priorité de cette fonction est dorénavant acceptée aussi bien pour le corps cardiaque que pour le tissu chloragogène, mais son intervention peut intéresser aussi bien la dégradation et peut-être le recyclage du pigment respiratoire que sa biosynthèse. A côté de l'accumulation de produits accessoires décrite par KENNEDY & DALES (1958) comme le résultat du catabolisme des métalloporphyrines, l'intervention possible des corps cardiaques dans des processus de détoxification a été évoquée dans leur potentialité de séquestration d'éléments exogènes figurés ou non (BRAUNBECK & DALES, 1984). Enfin, dans les incertitudes même de son utilisation, le concept de "chloragosome" prend en compte dans les travaux récents (OUAGHI & GRASSET, 1991) une possibilité de bioaccumulation progressive notamment du fer. Une telle bioaccumulation pourrait-elle être l'indice indirect d'un état physiologique modifié par la surcharge environnementale en hydrocarbures? A travers l'hypothèse d'une détoxification chez une espèce privilégiée, c'est donc aussi à l'interprétation du rôle du corps cardiaque en conditions normales que notre travail tente de contribuer.

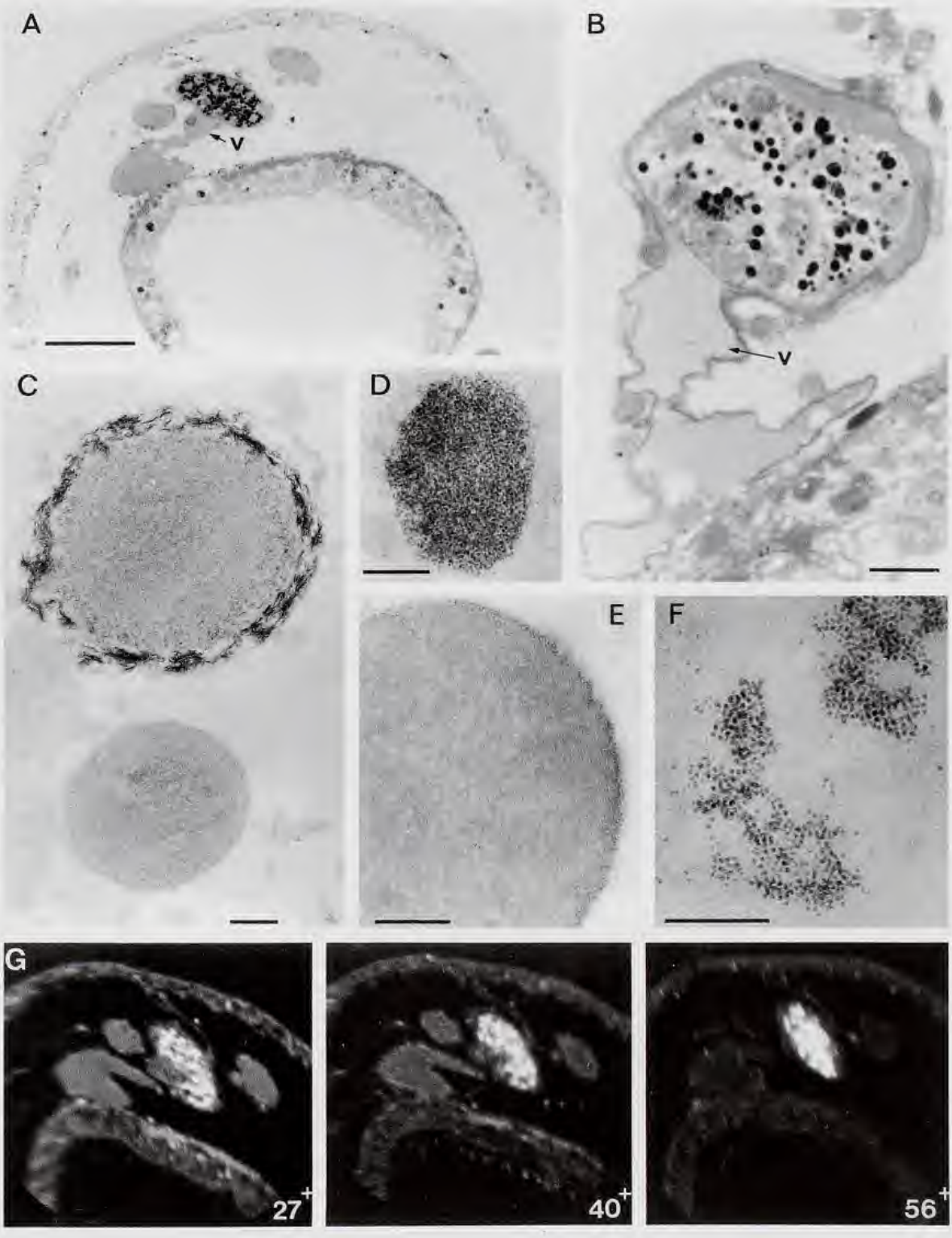
## MATÉRIEL ET MÉTHODES

Le matériel utilisé pour cette étude provient de deux récoltes différentes, l'une et l'autre de la mer du Nord septentrionale : l'une prélevée juste au nord ("close up N" = CU N) de la plateforme pétrolière Beryl (mai 1982), l'autre 200 mètres au nord (200 N) du point précédent (mai 1985). Les animaux ont été fixés au formol à 10 % et le prélèvement CU N a été ensuite transféré dans l'alcool éthylique à 80 °C.

Les spécimens examinés ont été tronçonnés au niveau du corps cardiaque (au delà du 9e sétigère) et inclus dans l'araldite après déshydratation à l'alcool. L'anatomie microscopique a été établie sur coupes transversales

FIG. 1. — A. Région dorsale (spécimen 15, CU N). Coupe transversale semi-fine colorée au bleu de Toluidine (barre 50 µm); v : espace sanguin ; B. Détail du corps cardiaque (spécimen13, 200 N), même préparation (barre 10 µm) ; C, D, E, F. Micrographies électroniques sans post-osmication ni coloration (barre 200 nm pour C et E, 100 nm pour D et F) ; C. Sphérule entourée d'aiguilles d'oxyde de fer (spécimen18 CU N), D. Granule de ferritine (spécimen 5, 200 N), E. Sphérule homogène enrichie superficiellement en ferritine (spécimen 4, 200 N), F. Particules intracytoplasmiques de ferritine (spécimen18, CU N), G. Images d'émission ionique (spécimen15, CU N). 27+ : Al, 40+ : Ca, 56+ : CaO + Fe (même échelle que A).

Source : MNHN, Paris




Source : MNHN, Paris

semi-fines colorées au bleu de toluidine, l'étude cytologique ultrastructurale sur coupes ultra-fines non colorées. La fixation initiale et le mode de conservation du matériel ne pouvaient permettre qu'une approche grossière des ultrastructures, excluant toute post-osmication et toute identification des organites et des membranes.

L'étude microanalytique a fait appel à trois instruments différents.

- sur coupes semi-fines, après montage sur terphane carboné, microsonde MS 46 Cameca équipée de spectrographes dispersifs en longueur d'onde à cristaux KAP et PET (diamètre de sonde l µm);
- sur coupes semi-fines étalées sur support de platine, microanalyseur ionique Cameca SMI 300 (spectres acquis sur tout le champ image, diamètre 250 µm);
- sur coupes ultra-fines montées sur grille de cuivre, microscope électronique Temscan JEOL JEM CXII équipé d'un détecteur de rayons X à sélection d'énergie (EDS) LINK modèle AN 10000 à cristal SI(LI). Tension d'accélération 60 kV. Surface analysée pour chaque spectre 50 x100 nm, temps de comptage 300 s.

Vingt-cinq individus ont été examinés à l'échelle photonique (15 pour 200 N, 10 pour CU N), 20 à l'échelle ultrastructurale, 18 en microanalyse par dispersion de longueur d'onde, permettant la sélection des quatre retenus pour la microanalyse par dispersion d'énergie et des deux étudiés au microanalyseur par émission ionique secondaire.

## RÉSULTATS

L'examen à la loupe des vers provenant des deux récoltes permet de reconnaître le corps cardiaque, dorsal et visible à travers l'épithélium, comme une ligne pigmentée plus ou moins sinueuse partant du 8 ou 9 ème sétigère et courant sur les 10 à 15 suivants. Brun noirâtre, il apparaît plus foncé et plus épais pour les individus provenant du lot CU N que pour ceux de 200 N.

ANATOMIE MICROSCOPIQUE ET HISTOLOGIE (Fig. 1A-B). — De section circulaire en coupe transversale, l'organe est suspendu entre l'épiderme et le tractus digestif par un mésothélium qui se dilate localement pour former un ou plusieurs vaisseaux. La masse compacte de cellules constituant le corps cardiaque baigne ainsi dans un espace vasculaire plus ou moins développé, délimité par une "basale" extracellulaire ("vascular lamina") supportant extérieurement les corps cellulaires d'un revêtement péritonéal (myomésothélium), et sans doute infléchie pour délimiter le pourtour du corps cardiaque. Ce dernier présente en coupe une douzaine de cellules à noyaux pourvu d'un gros nucléole, périphériques par rapport à leurs inclusions de taille et de contraste divers, certaines très opaques, d'autres jaunâtres et translucides.

KENNEDY & DALES (1958) ayant signalé l'éventualité du développement du corps cardiaque avec l'âge et la bioaccumulation, nous avons comparé pour les deux lots de *Raricirrus* plusieurs systèmes indicateurs.

Les valeurs obtenues (n= nombre d'individus étudiés) ne marquent pas de différence significative en ce qui concerne :

- le diamètre du corps au niveau examiné :

200 N : 251 ± 16 µm, n = 5; CU N : 274 ± 18 µm, n = 7

- le diamètre du corps cardiaque :

200 N : 35 ± 9 µm, n = 14; CU N : 36 ± 8 µm, n = ll.

L'intégrité des cellules est identique dans les deux lots. Le développement de l'espace vasculaire périphérique est variable dans les deux lots, peut être plus souvent important pour CU N. Par contre, on reconnaît davantage d'inclusions claires pour 200 N.

CYTOLOGIE (Fig. 1C-D-E). — La préparation du matériel à notre disposition ne permet qu'une appréciation incomplète des ultrastructures : les membranes sont rarement identifiables, les noyaux et certains organites (mitochondries) altérés et on devine à peine certains trajets canaliculaires intracytoplasmiques. L'absence la plus regrettable concerne les vacuoles qui doivent concentrer le pigment respiratoire. Ceci accepté, on peut faire l'inventaire et la description de divers types d'inclusions, plus ou moins contrastées et dont l'opacité aux électrons est en partie attribuable à un métal présent naturellement, que la microanalyse désignera comme du fer.

La majorité des inclusions des cellules du corps cardiaque correspond dans les deux lots à des sphérules régulières de diamètre moyen 0,9 µm (jusqu'à 1,5 µm) d'un matériau homogène modérément contrasté, à la périphérie desquelles on devine parfois une membrane. Elles peuvent être regroupées en amas moruliformes (jusqu'à 2,5 µm), parfois cernées d'une couche externe moins dense et plus souvent, dans les deux lots, d'une zone contrastée de particules que nous reconnaîtrons comme de la ferritine (Fig. lE). Cette ferritine peut envahir complètement la sphérule dans une répartition régulière ou localisée.

Distincts des sphérules par leur contraste et leur diamètre moyen (0,3 µm, Fig. lD) des amas arrondis de ferritine, sans apparence de membrane périphérique, sont également présents dans les deux lots. Les particules

Source : MNHN, Paris

constitutives sont plus ou moins organisées, encore qu'on n'y observe jamais de plages pseudocristallines telles qu'on en connaît dans les inclusions comparables du tissu chloragogène des Sabellidae (OUAGHI,1989) et Serpulidae (VOVELLE *et al.* ,1991). On reconnaît dans les mêmes cellules des plages plus petites (0,2 µm) et moins organisées des mêmes particules, assurément intracytoplasmiques, à contours irréguliers (Fig. 1F). Ces particules "ferritin like" pour quelques auteurs (mais que nous confirmerons par la microanalyse) apparaissent isolément, en plus ou moins grande densité, dans l'ensemble du cytoplasme. À grossissement convenable, leur taille (environ 12 nm) et leur conformation fournissent un nouvel élément d'identification.

Une partie de ces inclusions est comparable à celles décrites par divers auteurs (i.a. FRIEDMAN & WEISS, 1980 ; OUAGHI & GRASSET, 1991) dans les corps cardiaques et tissus chloragogènes de diverses Polychètes, et peut être interprétée dans le cycle de l'hématopoièse. Les sphérules homogènes sont originales et nous hésitons à leur donner un rapport de filiation avec les "granules de ferritine", même si elles peuvent se charger de particules. On les distingue en tout cas des inclusions claires lipidiques à membrane qu'on peut identifier dans quelques spécimens des deux lots.

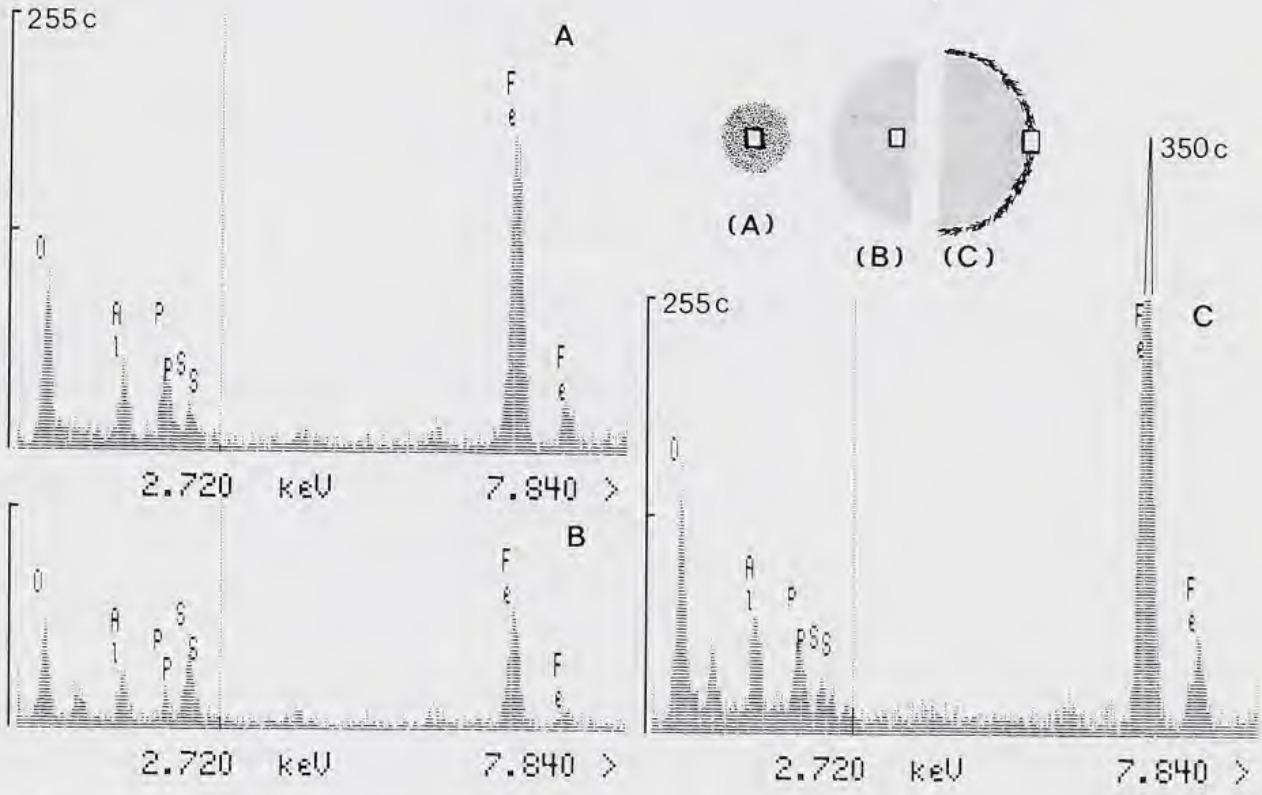



FIG. 2. — Microanalyse en sélection d'énergie sur coupes ultra fines (spécimen 18, CU N) A. Granule de ferritine, B. partie centrale d'une sphérule homogène, C. Feutrage d'aiguilles périphérique à une sphérule. Tension d'accélération 60 kV, temps de comptage 300 s. En blanc sur les schémas : surface analysée; c : nombre de coups.

Source : MNHN, Paris

Il appartient à deux individus sur neuf examinés dans le lot CU N de présenter une surcharge originale des sphérules homogènes : dans certaines plages cellulaires elles sont recouvertes sur une épaisseur de 0,1 µm d'un feutrage d'aiguilles à fort contraste, alors que leur matière fondamentale est souvent chargée de particules de ferritine (Fig. 1C). Ces aiguilles de dimension moyenne 50 nm évoquent celles que nous avons décrites en filiation d'inclusions de ferritine dans la biominéralisation cuticulaire des mâchoires d'un Eunicien (VOVELLE *et al.*, 1989) ou celle que COULON *et al.* (1987) ont reconnues dans des conditions de pollution naturelle à la surface des filaments de byssus de moules. Ces auteurs y ont identifié des oxydes métalliques (hématite principalement) et cette interprétation est à prendre en compte pour notre matériel.

MICROANALYSE. — *Spectrométrie de rayons X en dispersion de longueur d'onde.* On a d'abord examiné deux individus différents dans chacun des lots. Les éléments présents ont été reconnus et appréciés à partir de moyennes établies sur une dizaine de points (1 µm environ) particulièrement émissifs dans deux ou trois coupes voisines de chaque échantillon. Les éléments reconnus sont en ordre d'importance Fe, S, Ca, P, Al et Cu (traces). La recherche de Zn et V, suggérée par leur existence dans le tissu chloragogène des Serpulidae, n'a pas donné de réponse significative. Les valeurs obtenues pour Al ne présentent pas de variation notable entre les deux lots (non plus que celles de Cu). Les valeurs moyennes concernant les éléments majeurs ont été comparées aux valeurs maximales obtenues pour chaque échantillon, par rapport auxquelles elles sont minorées dans la proportion d'un tiers. Si on compare les deux lots, les moyennes pour Ca et P sont majorées pour le site CU N, et encore plus en ce qui concerne S et surtout Fe.

Dans un deuxième temps on a donc apprécié systématiquement, en retenant les mêmes définitions de valeurs moyennes, l'intensité de réponse du fer, en parallèle avec celle du soufre, pour 9 individus du lot CU N et 7 du lot 200 N. Les valeurs moyennes et maximales pour Fe sont multipliées par trois pour la récolte la plus proche de la station Beryl. Ceci représente une moyenne de :

CU N : 145 ± 60 c/s (max. 252), contre 200 N : 58 ± 31 c/s (max. 89).

En ce qui concerne le soufre, les valeurs obtenues sont :

CU N : 43 ± 17 c/s (max. 58), contre 200 N : 25 ±10 c/s (max. 36).

Le soufre ne présente donc pas une évolution aussi marquée que le fer. Si l'on compare les valeurs obtenues à celles concernant le tissu chloragogène et le corps cardiaque des Sabellidae, Serpulidae et Amphictenidae (VOVELLE *et al.*, 1991), elles apparaissent plus faibles, car obtenues sur coupes semi-fines, mais surtout la participation du phosphore est minorée, celle du soufre plus importante.

*Microanalyse par émission ionique secondaire.* Les renseignements exploités concernent les spectres d'émission d'ions secondaires positifs et négatifs et les images obtenues pour les éléments les plus émissifs. Un individu de chaque lot a été examiné.

Sur les spectres d'émission les éléments identifiés sont par ordre d'importance Ca (40+), Fe (56+), Al (27+), S (32-), Cl (35 ) imputable en partie à la résine, P mal servi par la méthode mais présent dans diverses combinaisons (POCa 87+), Mg (24+) et Cu (63+) comme intervenants mineurs, et F (19 ) en traces. Ces évaluations intègrent l'analyse d'une surface de 200 µm de diamètre, supérieure à celle de l'organe en coupe.

L'analyse des images obtenues à partir des masses présentant la meilleure intensité d'émission, 56+, 40+, 27+ (Fig. 1G), impose qu'on tienne compte du contraste entre l'organe considéré et les tissus environnants, pour apprécier une concentration locale de l'élément identifié. La masse 56+ imputable à Fe plus qu'à CaO présente le meilleur contraste, alors que Ca et surtout Al sont présents dans les autres parties de la coupe.

Même si la réponse du fer est meilleure sur l'échantillon provenant du lot CU N, cette méthode ne permet pas d'apprécier quantitativement des différences significatives entre les vers des deux provenances.

*Spectrométrie de rayons X en sélection d'énergie.* Cet examen à l'échelle ultrastructurale sur coupes fines fournit des spectres correspondants pour les divers types d'inclusions à des surfaces analysées de 100 X 50 nm. Une approximation de l'importance relative des divers éléments présents dans chacun d'eux a été obtenue pour deux échantillons de chaque lot en comparant l'importance des pics obtenus dans des conditions identiques, exprimée en coups. Les éléments reconnus correspondent dans l'ordre d'importance aux pics Fe, 0, Al, S, P et Ca. On les identifie dans les accumulations de ferritine, dans les sphérules homogènes et dans le feutrage d'aiguilles périphérique à certaines sphérules du lot CU N.

En ce qui concerne le fer, la réponse maximale est de 35 ± 9 coups dans le cytoplasme, 86 ± 18 et 102 ± 39 coups au centre des sphérules homogènes claires (200 N et CU N), mais les sphérules chargées de ferritine peuvent en présenter davantage, 183 ± 36 (200 N) et 155 ± 20 (CU N) dans les amas arrondis de ferritine, jusqu'à 277 ± 80 dans le feutrage périphérique (CU N).

Source : MNHN, Paris

La présence de l'oxygène, notable sur les spectres, est contingente du carbonage des grilles. Celle de l'aluminium est confirmée dans tous les cas, sans indication d'accumulation particulière dans les sphérules, ni de différence marquée selon les provenances.

Le rapport du phosphore au soufre est significatif, leurs deux pics sont alternativement prépondérants. Le phosphore est plus important que le soufre dans les accumulations de ferritine, ce qui n'est pas aussi net dans les feutrages en aiguilles. Le soufre (organique?) a la priorité au centre des inclusions sphérulaires. La présence du phosphore dans la ferritine est généralement acceptée ; nous interprétons celle du soufre dans les sphérules clairs en rapport avec une composante protéique probable, comportant des acides aminés soufrés.

## DISCUSSION ET CONCLUSIONS

Les trois méthodes de microanalyse utilisées ne concernent pas le même champ dimensionnel, l'une présentant la répartition des éléments dans l'animal, l'autre dans l'organe, la dernière au niveau ultrastructural des inclusions cellulaires. Leurs performances mais aussi leurs déficiences par rapport à certains éléments se complètent. La convergence des résultats obtenus permet de proposer un inventaire des éléments majeurs concentrés par le corps cardiaque : fer, calcium, soufre et phosphore, les éléments mineurs ou traces ne présentant aucun caractère original. La présence notable de l'aluminium est confirmée par les trois méthodes, elle concerne l'ensemble des tissus de l'animal sans enrichissement considérable au niveau du corps cardiaque, ni différence marquée entre les deux sites. S'agit-il d'un élément artefactuel, induit par une des manipulations préparatoires ? Il est impossible actuellement de le démontrer. Les éléments reconnus dans les deux lots de provenance différente sont identiques. Ils sont tous interprétables en rapport avec une fonction hématopoiétique de l'organe. La seule donnée apportée par l'étude de microanalyse (microsonde MS 46) pour différencier les vers de CU N et de 200 N concerne l'abondance du fer dans le corps cardiaque dont la valeur triple à proximité de la plateforme, sans qu'aucun autre élément ne présente une bioaccumulation corrélative.

Cette surcharge imputable à un seul métal impliqué dans le métabolisme du pigment respiratoire est en bon accord avec deux autres données, morphologique et ultrastructurale. Morphologiquement il s'agit de l'indice de départ, l'intensité de la pigmentation brun noir de l'organe, renforcée pour le lot CU N. A l'échelle ultrastructurale il s'agit de la présence spécifique dans des individus du même lot de dépôts ferriques en aiguilles périphériques à certaines inclusions. Cette forme d'accumulation du métal, dont la réversibilité est moins évidente que pour la ferritine, évoque une surcharge qu'on peut raisonnablement mettre en rapport avec une hématopoièse et un cycle du pigment respiratoire sollicités par les conditions environnementales. Les conditions de conservation des animaux ne permettent pas de décrire davantage la cytophysiologie des corps cardiaques de *Raricirrus*, qui pourra être précisée dans une étude ultérieure, mais elles nous autorisent déjà à envisager un rapport entre cette forme spécifique de bioaccumulation du fer et un processus de détoxification des animaux exposés à un milieu riche en hydrocarbures.

## BIBLIOGRAPHIE

BRAUNBECK, T. & DALES, R. P., 1984. — The role of the heart body and of the extravasal tissue in the disposal of foreign cells in two polychaete annelids. *Tissue & Cell*, **16** : 557-563.

COULON, J., TRUCHET, M. & MARTOJA, R., 1987. — Chemical features of mussels (*Mytilus edulis*) *in situ* exposed to an effluent of the titanium dioxyde industry. *Annls Inst. Océanogr.*, **63** : 89-100.

FRIEDMANN, M.M. & WEISS, L., 1980. — An electron microscopy study of hemoglobin synthesis in the marine annelid *Amphitrite ornata* (Polychaeta Terebellidae). *J. Morphol.*, **164** : 121-138.

KENNEDY, G.Y. & DALES, R. P., 1958. — The function of the heart-body in the Polychaetes. *J. mar. biol. Ass. U.K.*, **37** : 15-31.

MOORE, D.C., 1991. — *Raricirrus beryli* Petersen & George (Ctenodrilidae): a new Polychaete indicator species from hydrocarbon-polluted sediments. *Ophelia* Suppl., **5** : 447-486.

OUAGHI, E. M., 1989. — Bioaccumulation naturelle du fer chez *Sabella pavonina* S. (Annélide Polychète). *C.R. Acad. Sci. Paris*, **308** : 237-244.

OUAGHI, E. M. & GRASSET, M., 1991. — Synthèse et exocytose de chlorocruorine et mise en réserve du fer par le tissu périvasculaire d'un annélide polychète. *Can. J. Zool.*, **69** : 2338-2348.

Source : MNHN, Paris

PETERSEN, M. E. & GEORGE, J. D., 1991. — A new species of *Raricirrus* from northern Europe, with notes on its biology and a discussion of the affinities of the genus (Polychaeta: Ctenodrilidae). *Ophelia,* Suppl., **5** :185-208.

VOVELLE, J., GRASSET, M. & TRUCHET, M., 1989. — Biominéralisation des mâchoires chez *Hyalinoecia tubicola* (Müller) (Polychète, Eunicida). *Annls Inst. Océanogr.*, **65** : 15-36.

VOVELLE, J., GRASSET, M. & TRUCHET, M., 1991. — Sites of biomineralization in the Polychaete *Pomatoceros triqueter* (Serpulidae) with comments on some other species. *Ophelia,* Suppl., **5** : 661-667.

Source : MNHN, Paris

# Functional ciliary groups of the feeding palps of Spionid polychaetes

*Daniel M. DAUER*

Department of Biological Sciences
Old Dominion University
Norfolk, Virginia, USA 23529

ABSTRACT

Functional ciliary groups of the feeding palps of spionid polychaetes are reviewed. Six functional ciliary groups have been observed: frontal cilia, latero-frontal cirri, lateral cilia, ciliated papillae, non-motile cilia of the frontal surface and basal transverse cilia. The number of functional ciliary groups present on any species varies from one to four groups. Some ciliary groups, e.g. frontal cilia, are present on the palps of many species while other groups, e.g. basal transverse cilia, are unique to a single species. Additional studies are necessary to clarify the roles of and possible interactions between (1) functional ciliary groups, (2) mucus and (3) hydrodynamics in particle encounter, retention, transport and rejection.

RÉSUMÉ

**Groupes ciliaires fonctionnels des palpes "trophiques" des polychètes Spionidae**

Une révision des groupes ciliaires fonctionnels des palpes "nutritionnels" des polychètes Spionidae est entreprise. Six groupes ciliaires fonctionnels ont été observés : cils frontaux, cirres latéro-frontaux, cils latéraux, papilles ciliées, cils non mobiles de la surface frontale et cils transverses frontaux. Le nombre de groupes ciliaires fonctionnels présents chez chacune des espèces varie de un à quatre. Quelques groupes ciliaires, comme les cils frontaux, sont présents sur les palpes de beaucoup d'espèces tandis que d'autres groupes, comme les cils transverses basaux, ne sont présents que chez une espèce. Des études complémentaires sont nécessaires pour clarifier les rôles et les interactions possibles entre (1) groupes ciliaires fonctionnels, (2) mucus, (3) hydrodynamique dans la rencontre, la rétention, le transport et le rejet des particules.

## INTRODUCTION

Spionid polychaetes are common inhabitants of infaunal and epifaunal communities of marine and estuarine habitats. The ciliated peristomial palps of spionid polychaetes function in (1) feeding behavior (FAUCHALD & JUMARS, 1979), (2) inter- and intraspecific interactions (LEVIN, 1981) and (3) tube construction (MORTENSEN & GALTSOFF, 1944). In feeding behavior the palps may function in particle encounter, retention, transport, and rejection (e.g. TAGHON *et al.*, 1980; DAUER *et al.*, 1981). Spionid polychaetes use their palps to capture particles in suspension, bedload transport and deposited at the sediment surface; direct deposit feeding using the everted

DAUER, D.M., 1994. — Functional ciliary groups of the feeding palps of Spionid polychaetes. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 81-84. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

pharynx has also been observed (DARO & POLK, 1973; WILSON, 1983). The potential rapid flux between suspended, bedload, and deposited states caused DAUER *et al.* (1981) to classify spionids as interface feeders. In this paper studies concerning the role of cilia on the palps are reviewed and areas of future research discussed.

## DISTRIBUTION OF FUNCTIONAL CILIARY GROUPS WITHIN AND BETWEEN SPECIES

Studies combining feeding behavior and detailed morphological observations have been performed for eight spionid species and Table 1 summarizes the distribution of ciliary groups among these species. Spionid polychaetes with a median ciliated food groove have one or more of the following five functional groups of cilia on their palps: (1) frontal cilia that line the median groove of the palp, (2) latero-frontal cilia organized as compound cilia (cirri), (3) lateral cilia that beat in metachronal waves, (4) non-motile cirri located at the tips of papillae, and (S) basal transverse cilia at the base of the palp. Within a species, the number of functional ciliary groups varies from one to four. For example, *Malacoceros indicus* has only frontal cilia lining the food groove (DAUER & EWING 1991) and *Paraprionospio pinnata* has four ciliary groups - frontal cilia, latero-frontal cirri, lateral cilia and basal transverse cilia (DAUER, 1985). Between species, some ciliary groups, e.g. frontal cilia, are present on the palps of many species while other groups, e.g. basal transverse cilia, are unique to a single species. *Scolelepis squamata* and *S. hutchingsae* lack a median food groove and the cilia of the palps are non-motile and organized into numerous transverse rows (DAUER, 1983, 1987).

TABLE 1. — Distribution of ciliary groups among the Spionidae.
(from 1- DAUER, 1983; 2- DAUER, 1984; 3- DAUER, 1985; 4 - DAUER, 1987; 5 - DAUER, 1991; 6 - DAUER & EWING, 1991).
X: ciliary or cirral group is present. —: ciliary or cirral group is absent.

| Species | Frontal Cilia | Latero Frontal Cirri | Papillae | Lateral Cilia | Non-Motile Cilia | Basal Transverse Cilia |
|---|---|---|---|---|---|---|
| *Malacoceros indicus* [6] | X | — | — | — | — | — |
| *Polydora commensalis* [5] | X | — | X | — | — | — |
| *Polydora ligni* [4] | X | X | X | — | — | — |
| *Polydora websteri* [4] | X | X | X | — | — | — |
| *Streblospio benedicti* [2] | X | X | — | X | — | — |
| *Paraprionospio pinnata* [3] | X | X | — | X | — | X |
| *Scolelepis hutchingsae* [4] | — | — | — | — | X | — |
| *Scolelepis squamata* [1, 4] | — | — | — | — | X | — |

## FEEDING BEHAVIOR

The ciliary groups of the palps of spionid polychaetes may function in particle encounter, retention, transport, and rejection. Particle capture implies particle encounter and subsequent retention. Particle transport implies the movement from the site of capture to the pharynx. Particle rejection implies that the particle is not ingested after capture and would include loss during transport as well as transport away from the pharynx.

Particle encounter in the deposit feeding mode occurs as the frontal surface of the palp is placed onto the sediment surface and can be predicted as a function of particle size with larger particles having a higher probability of being encountered (JUMARS *et al.*, 1982). In the suspension feeding mode, particle encounter prediction is a function of encounter mechanism (direct interception, inertial impaction, gravitational deposition, diffusional deposition, electrostatic attraction, SHIMETA & JUMARS, 1991). The frontal surface of the palp is the site of particle encounter, but the ciliary groups of Table 1 probably have no role in particle encounter dynamics of deposit feeding and could only have a role in suspension feeding if currents produced by the cilia of the palps altered ambient flow conditions. DAUER (1984, 1985) hypothesized that both the latero-frontal cirri and lateral cilia of *P. pinnata* and *Streblospio benedicti* created currents that increased particle encounter during suspension feeding. Ciliary currents would be functional only in low ambient flows such as in highly depositional environments or close to the sediment surface in the bottom boundary layer.

Source : MNHN, Paris

Retention of particles in spionid polychaetes is assumed to be due to the adhesive properties of mucus secreted on the frontal surface and the interaction of mucus and surface properties of the particle (roughness, organic coatings) (JUMARS *et al.*, 1982). Hydrodynamic particle retention, produced by cilia of the palps *(sensu* JORGENSEN 1981, 1982), again could only occur under low ambient flow conditions or when the collection surface is sheltered from ambient flow (SHITEMA & JUMARS, 1991). Mucus is particularly important in particle retention of the *Scolelepis* spp. The non-motile cilia of the *Scolelepis* spp. were interpreted by DAUER (1983, 1987) as providing a rough textural surface to retain the particle-mucus complex which was transported to the pharynx by complete retraction of the palp frontal surface directly onto the pharyngeal surface. DAUER (1987) hypothesized this mechanism was an adaptation to the highly turbulent habitat occupied by both species and minimized the loss of particles during transport along the food groove of the palp as envisioned by SELF & JUMARS (1978). Particle retention during transport can also be a function of the depth of the food groove. For example, in *P. pinnata* the food groove is deep and wide and particles up to 100 µm in greatest dimension were completely enc-losed by the lateral edges of the frontal surface during transport to the pharynx (DAUER, 1985). Particles less than 100 µm make of the vast majority of particles ingested by *P. pinnata* (DAUER, 1980; LUCKENBACH *et al.*, 1988).

Particle transport to the pharynx, as a particle-mucus complex, is primarily accomplished by the beating of the frontal cilia in those spionids with a median food groove. For the *Scolelepis* spp. the non-motile cilia of the frontal surface serve indirectly in particle transport by holding the particle-mucus complex onto the frontal surface as the palp contracts onto the pharynx (DAUER, 1983).

Frontal cilia may also function in particle rejection from the pharynx by a reversal of the direction of ciliary flow. This mechanism has been observed only in *Polydora ligni* (DAUER *et al.*, 1981). The basal transverse cilia of *P. pinnata* function in particle rejection by the production of a rejection current within the tube. Particles rejected at the site of the pharynx are rejected into the current produced by the beating of the basal transverse cilia and the frontal cilia of the branchiae (DAUER, 1985). DAUER (1988) hypothesized that the particle rejection current of *P. pinnata* enabled the animal to reject particles at the site of the pharynx while allowing the prostomium to remain below the sediment-water interface and thus potentially reducing predation or browsing. In other spionid species the everted pharynx is held at the sediment surface or the edge of the tube and particles are rejected directly onto the sediment-water interface.

The ciliated papillae of spionids do not appear to have any direct function in feeding behavior. DAUER (1991) hypothesized that the papillae of the palp are primarily mechanosensory structures that may be important in interspecific encounters.

The role of the lateral cilia and the latero-frontal cirri is particularly problematic. DAUER (1984, 1985) by analogy to lamellibranch bivalves and lophophores concluded that both ciliary groups functioned in capturing suspended particles by creating currents (lateral cilia) and deflecting the pathway of particles onto the frontal surface (latero-frontal cirri). SHITEMA & JUMARS (1991) consider that cilia that are not protected from ambient flow may be more important in manipulating and transporting captured particles rather than in creating feeding currents. Latero-frontal cirri could aid in retaining the particle-mucus complex onto the frontal surface during transport. However, it is difficult to hypothesize and role for the lateral cilia except for the creation of a feeding current. These cilia are adjacent to the frontal surface (to assist to particle retention) and beat in metachronal waves creating currents directed towards the frontal surface.

## CONCLUSION

Spionid polychaetes have been and will continue to be important experimental species in applying optimal foraging theory to marine and estuarine systems (TAGHON, 1982; TAGHON & JUMARS, 1984) and in understanding the role of near-bottom hydrodynamics in feeding behavior (JUMARS, 1993). Spionid polychaetes are excellent experimental subjects for feeding studies because (1) they feed at the sediment-water interface and are easily observed, (2) many spionid species, especially estuarine species, are relatively hardy and survive well under laboratory experimental conditions, and (3) most species place fecal rods at the surface which can be collected and used to estimate feeding rates quantitatively under various experimental conditions. However, interpretation of data and observations concerning feeding of spionids is complicated because (1) they have a mixed feeding mode (deposit feeding, suspension feeding, bedload feeding) and (2) they posses a variety of morphological features that may affect feeding behavior. Additional studies are necessary to clarify the roles of and possible interactions between (1) functional ciliary groups, (2) mucus and (3) hydrodynamics in particle encounter, retention, transport and rejection.

Source : MNHN, Paris

DARO, M.N. & POLK, P., 1973. — The autecology of *Polydora ciliata* along the Belgian coast. *Neth. J. Sea Res.*, **6** : 130-140.

DAUER, D.M., 1980. — Populations dynamics of the polychaetous annelids of an intertidal habitat in Upper Old Tampa Bay, Florida. *Int. Rev. Ges. Hydrobiol.*, **65** : 461-487.

DAUER, D.M., 1983. — Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: Spionidae). *Mar. Biol.*, **77** : 279-285.

DAUER, D.M., 1984.—Functional morphology and feeding behaviour of *Streblospio benedicti* (Polychaeta; Spionidae). *In*: P.A. HUTCHINGS (ed), *Proceedings of the First International Polychaete Conference*. Published by the Linnean Society of New South Wales: 418-429.

DAUER, D.M., 1985. — Functional morphology and feeding behavior of *Paraprionospio pinnata* (Polychaeta: Spionidae). *Mar. Biol.*, **85** : 143-151.

DAUER, D.M., 1987. — Potential systematic significance of spionid polychaete tentacular morphology. *Bull. biol. Soc. Wash.*, **7** : 41-45.

DAUER, D.M., 1991. — Functional morphology and feeding behavior of *Polydora commensalis* (Polychaeta: Spionidae). *Ophelia* Supplement **5** : 607-614.

DAUER, D.M. & EWING, R.M., 1991. — Functional morphology and feeding behavior of *Malacoceros indicus (Polychaeta:* Spionidae). *Bull. mar. Science*, **48** : 395-400.

DAUER, D.M., MAYBURY, C.A. & EWING, R.M., 1981. — Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.*, **54** : 21-38.

FAUCHALD, K. & JUMARS,P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Ann. Rev.*, **17** : 193-284.

JORGENSEN, C.B., 1981. — A hydromechanical principle for particle retention in *Mytilus edulis* and other ciliary suspension feeders. *Mar. Biol.*, **61** : 277-282.

JORGENSEN, C.B., 1982. — Fluid mechanics of the mussel gill: the lateral cilia. *Mar. Biol.*, **70** : 275-281.

JUMARS, P.A., 1993. — *Concepts in biological oceanography. An interdisciplinary primer*. Oxford University Press, New York. 348 pp.

JUMARS, P.A., SELF , R.F.L. & NOWELL, A.R.M., 1982. — Mechanics of particle selection by tentaculate deposit-feeders. *J. Exp. Mar. Biol. Ecol.*, **64** : 47-70.

LEVIN, L.A., 1981. — Dispersion, feeding behavior and competition in two spionid polychaetes. *J. mar. Res.*, **39** : 99-117.

LUCKENBACH, M.W., HUGGETT , D.V. & ZOBRIST, E.C., 1988. — Sediment transport, biotic modifications and selection of grain size in a surface deposit-feeder. *Estuaries*, **11** : 134-139.

MORTENSEN, E. & GALTSOFF, P., 1944. — Behavior and tube building of *Polydora ligni. Biol. Bull.* (Woods Hole), **87** : 164-165.

SELF, R.F.L. & JUMARS, P.A., 1978. — New resource axes for deposit feeders ? *J. mar. Res.*, **36**: 627-641.

SHIMETA, J. & JUMARS, P.A., 1991. — Physical mechanisms and rates of particle capture by suspension feeders. *Annual Rev. Oceanogr. mar. Biol.*, **29** : 191-257.

TAGHON, G.L., 1982. — Optimal foraging by deposit-feeding invertebrates: roles of particle size and organic coating. *Oecologia*, **52** : 295-304.

TAGHON, G.L. & JUMARS, P.A., 1984. — Variable ingestion rate and its role in optimal foraging behavior of marine deposit feeders. *Ecology*, **65** : 549-588.

TAGHON, G.L., NOWELL, A.R.M. & JUMARS,P.A., 1980. — Induction of suspension feeding in spionid polychaetes by high particle fluxes. *Science*, **210** : 562-564.

WILSON, H.H., Jr. 1983. — The role of density dependence in a marine infaunal community. *Ecology*, **63** : 295-306.

Source : MNHN, Paris

# Attributes of ribosomal DNA in alvinellid polychaetes from hydrothermal vents

*David R. DIXON *, Linda R.J. DIXON * & Verena TUNNICLIFFE ***

* Plymouth Marine Laboratory & Marine Biological Association
Citadel Hill
Plymouth PL1 2PB, UK
** School of Earth and Ocean Sciences
University of Victoria
B.C. Canada V8W 2Y2

ABSTRACT

The ribosomal DNA (rDNA) of three alvinellid polychaetes, *Paralvinella palmiformis* Desbruyères & Laubier, *P. pandorae* Desbruyères & Laubier and *P. sulfincola* Desbruyères & Laubier, from deep-sea hydrothermal vents in the eastern Pacific Ocean, has been subjected to restriction-endonuclease digestion and the resulting restriction fragments compared with those of *Melinna palmata* Grube, a member of a closely-related polychaete family, the Ampharetidae. An interesting feature of the rDNA of representatives of both polychaete families was the tendency to cut with restriction enzymes containing an increased number of G-C (guanine-cytosine) bases in their recognition sequences. Increased GC-content is known to confer greater thermal and chemical resistance to the DNA molecule. This apparent similarity between the chemical composition of rDNA of representative alvinellids and *Melinna palmata*, a shallow-water species which tolerates highly-reduced and metal-rich sediments, suggests that this character may have arisen in the distant past primarily as an adaptation to chemically stressed environments.

RÉSUMÉ

**Caractéristiques de l'ADN ribosomal de Polychètes Alvinellidés des sources hydrothermales**

Les ADN ribosomaux (ADNr) de trois polychètes alvinellidés, *Paralvinella palmiformis* Desbruyères & Laubier, *P. pandorae* Desbruyères & Laubier et *P. sulfincola* Desbruyères & Laubier, provenant des sources hydrothermales profondes de l'est pacifique, ont été digérés par une endonucléase de restriction. Les fragments obtenus ont été comparés avec ceux de *Melinna palmata* Grube, une annélide polychète proche de la famille des alvinellidés, les ampharetidés. Un aspect important de l'ADNr des polychètes est leur tendance à se couper avec les enzymes de restriction contenant un nombre important de séquence de bases G-C (Guanine-Cytosine) dans leurs segments de reconnaissance. L'augmentation de la séquence en G-C est connue pour conférer à l'ADN une plus grande résistance thermique et chimique. Cette apparente similarité entre la composition chimique de l'ADNr représentatif des alvinellidés et *Melinna palmata*, une espèce d'eau peu profonde qui tolère les sédiments fortement réduits et chargés en métaux, suggèrent que ce caractère a dû se développer dans le passé comme une adaptation au stress chimique de l'environnement.

---

DIXON, D.R., DIXON, L.R.J. & V. TUNNICLIFFE, 1994. — Attributes of ribosomal DNA in alvinellid polychaetes from hydrothermal vents. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 85-92. Paris ISBN 2-85653-214-4-165-2.

Source : MNHN, Paris

## INTRODUCTION

The polychaete family Alvinellidae is known only from hydrothermal vents in the Pacific Ocean (DESBRUYÈRES & LAUBIER, 1991). Two genera are described : *Alvinella* with two species and *Paralvinella* with nine species at vent sites on both sides of the Pacific. *Alvinella* species inhabit the sides of smokers on the East Pacific Rise only and they have substantial morphological alteration such as the insertion of bacterial filaments on the dorsum. The smoker habitat on Juan de Fuca Ridge and Marianas back-arc basin is occupied by *Paralvinella sulfincola* Desbruyères & Laubier and *Paralvinella hessleri* Desbruyères & Laubier, respectively. Other paralvinellid species live among vestimentiferan tubes or in sediments where the potential for high temperature encounters is low.

The alvinellid family has several characteristics reminiscent of the hypothetical ancestor of the terebellomorph order. The current model of systematic relationships among the alvinellid species is based on morphological analyses (DESBRUYÈRES & LAUBIER, 1991). *Alvinella* is the most derived genus. Within *Paralvinella*, there are four distinct morphological subgroups: *P. pandorae* is the most distinct and nearest the ancestral form while *P. palmiformis* and *P. sulfincola* belong to one subgroup marked by the form of the buccal tentacles. Although the latter two species share many features and are often collected together, genetic distance based on allozymes clearly differentiates the species (TUNNICLIFFE et al., in press).

This study examines three species from the Juan de Fuca Ridge: *Paralvinella pandorae pandorae* Desbruyères & Laubier, *P. palmiformis* Desbruyères & Laubier and *P. sulfincola* Desbruyères & Laubier. Habitat observations suggest that there is a preference for habitats with vent temperatures increasing in the order listed (Fig. 1). *P. p. pandorae* builds mucous sheaths in vestimentiferan clumps while *P. palmiformis* is sedentary but free-ranging in these lower temperature clumps and on sulphide chimneys formed by high temperature fluids (TUNNICLIFFE *et al.*, 1985; DESBRUYÈRES & LAUBIER, 1986). *P. sulfincola* is only found on sulphide chimneys and, in the greatest numbers, within centimetres of superheated fluids (TUNNICLIFFE *et al.*, in press). Observations of the proximity of certain species to fluid flows in excess of 100 °C challenge current dogma that molecular stabilisation in metazoans requires temperatures less than 60 °C (BROCK, 1985).

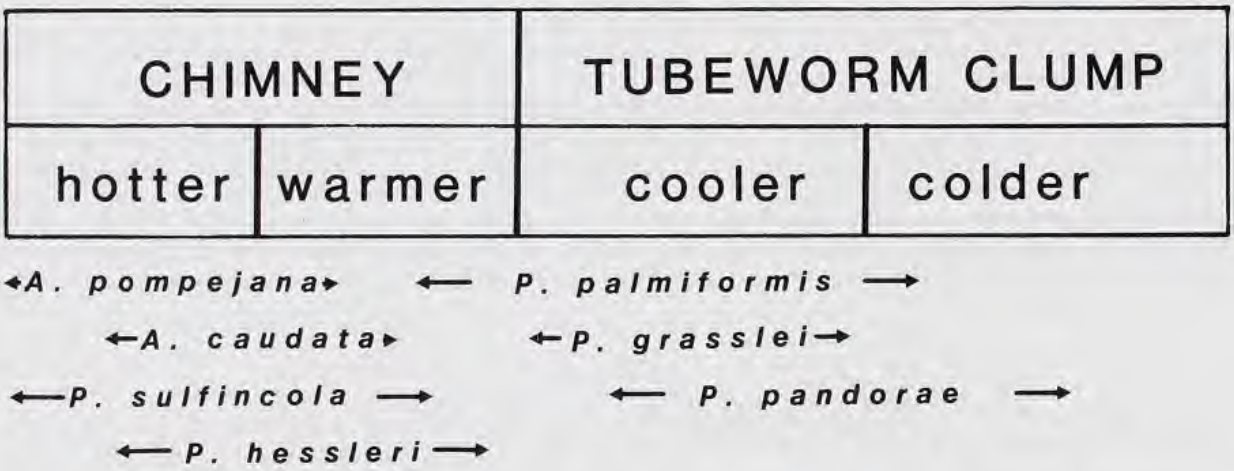



FIG. 1. — Approximate habitat ranges of alvinellid species. Hotter temperatures may range up to 65 °C as turbulent mixing carries blasts of hot water over the worms. There are no long-term records of chimney habitat temperatures to document actual ranges. Spot measurements and observations are the bases for this diagram. Little information is available for *P. hessleri*.

We recently reported the results of experiments which showed thermal stability of rDNA from a range of hydrothermal vent species (largely alvinellid polychaetes) was positively correlated with environmental temperature (DIXON *et al.*, 1992). This was attributed to a supposed increase in G-C (guanine-cytosine) content of the rDNA molecule. Increased G-C content confers increased thermal and chemical stability to the DNA molecule which is dependent on the number of hydrogen bonds: A-T (adenine-thymine) base pairs are linked by two bonds

Source : MNHN, Paris

whereas G-C pairs are linked by three (e.g. DARNELL *et al.*, 1986). This paper presents further evidence, based on restriction analysis results, of increased G-C levels in the rDNA of hydrothermal vent polychaetes and a close relative from highly-reduced and metal-rich, shallow-water environments, which suggests this character may have arisen in the distant past primarily as an adaptation to hostile chemical conditions.

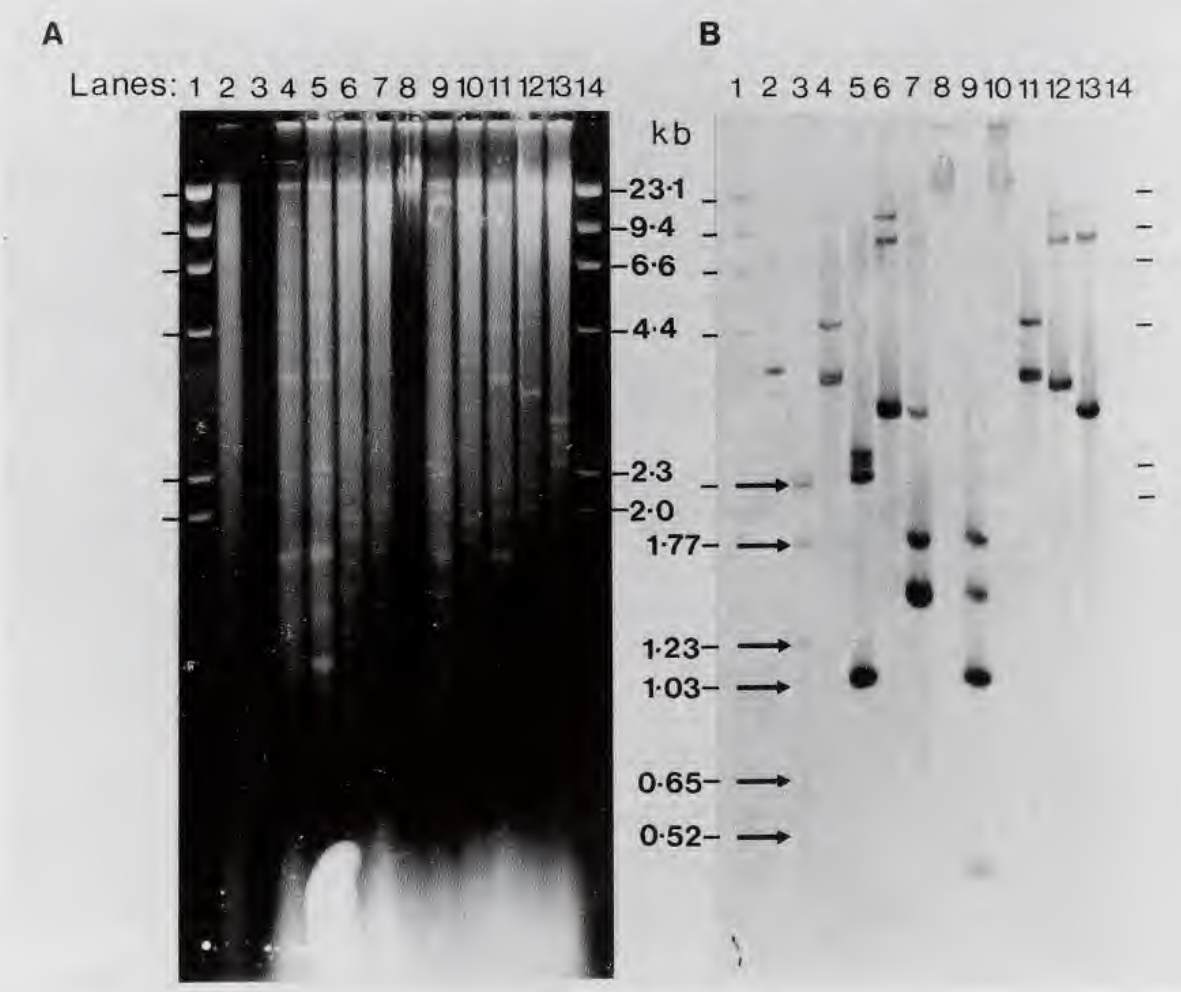



FIG. 2. — Hybridisation analysis of genomic DNA from a single *Paralvinella palmiformis*. (A) Photograph of 1% agarose gel after running at 30 volts for 16 h (0.1 volts $cm^{-1}$ $h^{-1}$) and ethidium-bromide staining, showing numerous satellite bands. (B) After Southern transfer and hybridisation with the 2.9 kb pVW-PCR (*P. palmiformis* rDNA-) digoxygenin-labelled probe. Lanes 1 and 14, Lambda-HindIII DNA molecular-weight marker; Lane 2, SalI-digested *Mytilus edulis* genomic DNA (control) showing a characteristic 3.6 kb fragment; Lane 3, DNA molecular weight marker, pBR328 cleaved with BglI and HinfI; Lanes 4 - 13, *P. palmiformis* genomic DNA: Lane 4, EcoRI/HindIII double digest; Lane 5, BamHI/EcoRI double digest; Lane 6, SalI/HindIII double digest; Lane 7, SalI/BamHI double digest. Note, suspected partial; Lane 8, undigested DNA; Lane 9, SalI/EcoRI double digest; Lane 10, HindIII digest showing absence of cutting sites within the repeat unit (cf. also lanes 6 and 13); Lane 11, EcoRI-digest; Lane 12, BamHI-digest; and Lane 13, SalI-digest.

Source : MNHN, Paris

## MATERIALS AND METHODS

*Specimen collection*

The three paralvinellid species were collected by submersibles on Juan de Fuca Ridge at two sites 100 km apart. Ten *P. palmiformis* specimens came from two vents on Axial Seamount (44°58.9' N, 130°13.3' W) and one vent on Cleft Segment (44°57.4'N, 130°13.8'W). The three *P. p. pandorae* specimens came from one vent at each site and *P. sulfincola*, two specimens, came from the base of a smoker at 44°58.9' N, 130°13.3' W. Another terebellomorph polychaete, the ampharetid *M. palmata* and the serpulid *Pomatoceros lamarckii* were collected subtidally at Plymouth, England; the dog-whelk *Nucella lapillus* and the mussel *Mytilus edulis* came from intertidal populations in southeast Cornwall.

*Tissue handling and DNA extraction*

High-molecular-weight DNA was purified by overnight digestion with proteinase K followed by repeated phenol/chloroform extractions. All DNA samples were treated with RNAse (SAMBROOK *et al.*, 1989). After ethanol precipitation, DNA was vacuum dried and dissolved overnight in TE (10 mM Tris, 1 mM EDTA, pH 8.0), and stored at 4°C for short periods or frozen at -20°C. Degraded DNA samples, identified by smearing on gels, were not included in the analysis.

*Restriction analysis*

Thirteen 6-cutter restriction endonucleases (Boehringer-Mannheim) were used singly and in combination on replicate samples of DNA : BamHI, Dra, EcoRI, EcoRV, HindIII, KpnI, PstI, PvuII, SacI, SalI, SmaI, XbaI and XhoI.

Approximately 2.5 mg of DNA was cut with restriction endonucleases according to the manufacturer's instructions. The DNA fragments were sorted according to size by gel electrophoresis using a 1 % agarose gel in TBE buffer (90 mM Tris-HCL, 0.89 mM boric acid, 2.5 mM EDTA, pH 8.3). Running conditions were 33 volts for 22 hours at room temperature. Gels were stained with ethidium bromide, photographed using UV-light, and the DNA blotted onto a nylon membrane (Genescreen, Dupont) (SOUTHERN, 1975).

*rDNA probes*

Homologous probes were manufactured by polymerase chain reaction (PCR), using PCR primers flanking regions 5 to the 18S and 28S genes (e.g. HOLLAND *et al.*, 1991), and cloned by conventional bacterial methods. A heterologous probe representing the entire rDNA repeat unit (pCtp 1550), (SCHMIDT *et al.*, 1982) was used after it had first been digested with HindIII and EcoRI to improve the labelling and hybridisation efficiencies. A non-radioactive DNA labelling and detection procedure was employed in this study (digoxygenin, KESSLER *et al.*, 1990).

## RESULTS

*Restriction analysis*

Figure 2 shows digestions of *P. palmiformis* rDNA with a range of restriction endonucleases, singly and in combination. Figure 2A is a representative agarose gel stained with ethidium bromide and photographed under UV-light to reveal numerous satellite bands. Fig. 2B shows the same panel of DNA when transfered to a nylon filter and labelled with a 2.9 kb VW- PCR probe (based on *P. palmiformis*, 5' 18S - 5' 28S rDNA region). The DNA fragments revealed by the probe(s) were used to map the rDNA repeat unit.

Table 1 shows the enzyme cutting results for three coastal and two hydrothermal-vent species. The probe used was pCtp 1550 (SCHMIDT *et al.*, 1982) which has the potential to span the entire length of the repeat unit. Repeat unit length was estimated for the different species based on the combined lengths of the fragments produced by SalI digestion. In the case of *M. palmata*, which lacks a SalI in its repeat unit, the size was estimated from the combined fragment sizes produced by separate BamHI, EcoRI, SacI and PstI digests. *M. edulis* DNA was the only one which cut with all 13 enzymes. With the exception of *M. palmata*, the number of enzymes which cut was inversely related to the size of the repeat unit. This relationship held when the comparison was made based on the size of the large non- transcribed spacer (NTS), indicating that the number of enzymes cutting was not simply a function of sequence length. Based on the number of G and C bases in the recognition sequences of the enzymes

Source : MNHN, Paris

which cut within the rDNA, the rDNA of the two hydrothermal vent polychaetes appears GC-rich, i.e. has a higher G-C index, compared to the three shallow-water species (Table 1).

TABLE 1.— Recognition sequences of restriction endonucleases, G-C indices (on a scale of 0 - 6), and individual species scores: *Paralvinella palmiformis*, (*P. palm.*); *P.p .pandorae*, (*P. pand.*); *Melinna palmata*, (*M. palm.*); *Nucella lapillus* (*N. lap.*); and *Mytilus edulis*, (*M. edulis*).

| Enzyme | Recognition sequence | G-C Index | *P. palm.* | *P. pand.* | *M. palm.* | *N. l ap.* | *M. edulis* |
|---|---|---|---|---|---|---|---|
| *Bam*HI | 5' -G'GATCC- 3' | 3 | + | + | + | + | + |
| *Dra*I | 5' -TTT'AAA- 3' | 0 | + | - | + | + | + |
| *Eco*RI | 5' -G'AATTC- 3' | 2 | + | + | + | + | + |
| *Eco*RV | 5' -GAT'ATC- 3' | 2 | - | - | - | + | + |
| *Hind*III | 5' -A'AGCTT- 3' | 2 | - | + | - | + | + |
| *Kpn*I | 5' -GGTAC'C- 3' | 4 | + | + | + | - | + |
| *Pst*I | 5' -CTGCA'G- 3' | 4 | - | - | + | - | + |
| *Pvu*II | 5' -CAG'CTG- 3' | 4 | + | + | + | + | + |
| *Sac*I | 5' -GAGCT'C- 3' | 4 | + | + | + | + | + |
| *Sal*I | 5' -G'TCGAC- 3' | 4 | + | + | - | + | + |
| *Sma*I | 5' -CCC'GGG- 3' | 6 | + | + | - | + | + |
| *Xba*I | 5' -T'CTAGA- 3' | 2 | - | - | - | + | + |
| *Xho*I | 5' -C'TCGAG- 3' | 4 | + | + | - | + | + |
| Enzymes cutting within the repeat unit, n: | | | 9 | 9 | 7 | 11 | 13 |
| Mean G-C Index: | | | 3.4 | 3.7 | 3.0 | 3.0 | 3.1 |
| G-C index of those enzymes that did not cut within the repeat unit. | | | 2.5 | 2.0 | 3.3 | 4.0 | - |

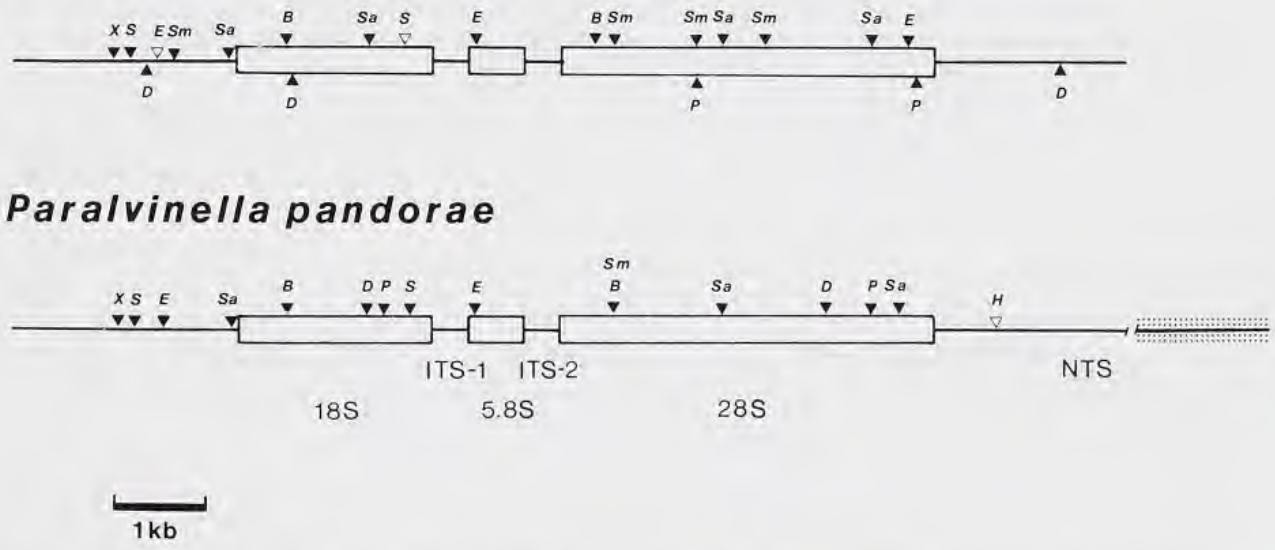



FIG. 3. — Restriction map of rDNA repeat unit of *Paralvinella palmiformis* and *P. pandorae*. Polymorphic restriction sites in *P. palmiformis* are indicated by open triangles. Restriction endonucleases which showed completely different cleavage patterns in the two species are shown below the restriction map of *P. palmiformis*. ITS-1 and ITS-2 = internal transcribed spacers; NTS = large non-transcribed spacer region; and 18S, 5.8S and 28S = the three rRNA-genes coding for the ribosomal subunits. B = BamHI; D = DraI; E = EcoRI; H = HindIII; P = PvuII; S = SalI; Sa = SacI; Sm = SmaI; and X = XhoI. The estimated 1.5 kb difference in repeat unit size was attributed to inter- specific variation in the size of the NTS region, indicated by the shaded portion in the map of *P. pandorae*. However, no enzyme was discovered which mapped to this region so confirmation must await the results of further investigations.

Source : MNHN, Paris

The three species of *Paralvinella* which were analysed for their rDNA structure had repeat unit lengths in the range 11 - 12.5 kb. This was significantly larger than the 7.2 - 7.6 kb values found for the three shallow-water species (one polychaete, two molluscs). The difference in repeat unit length between *P. pandorae* and *P. palmiformis* was traced to a duplication or some other sequence insertion affecting the NTS (Fig. 3). The significant differencein repeat unit length between *Melinna palmata* (7.5 kb) (Family Ampharetidae) and these three paralvinellids agrees with the conventional taxonomic separation of these two polychaete families.

*Restriction mapping*

Restriction sites for a total of eight enzymes were mapped for *P. palmiformis* and nine enzymes for *P. p. pandorae*; the extra one being HindIII (Fig. 3). These two species shared 10 restriction sites in common (37 %) out of a total of 27 mapped (Fig. 4). In contrast, *P. sulfincola* shared only four sites (22 %) in common with *P. palmiformis*, out of a total of 18 identified (DIXON & DIXON, unpublished), which may indicate a closer relationship between the former two species. (Note: insufficient high-quality DNA was extracted from the few specimens of *P. sulfincola* to carry out any detailed mapping of restriction sites.) Allowing for some heterogeneity between repeats and a degree of inter-individual restriction-site polymorphism, these data suggest that *P. palmiformis* is more closely related to *P. p. pandorae* than either is to *P. sulfincola*. Clearly, molecular adaptation to high temperature will have played an important part in speciation within this group. By way of contrast, the ampharetid *Melinna palmata* shared only six enzymes in common with the two paralvinellids (Table 1), and differed greatly in the number and size of fragments which these generated. The bulk of the variation in cleavage sites between *P. palmiformis* and *P. p. pandorae* mapped to genic regions within the rDNA repeat unit, although several polymorphisms were traced to the non-coding NTS. Lacking sequence information it is not possible to distinguish between introns and exons within genes. It seems highly probable that at least some of this intra-genic variation will involve "silent sequences", i.e. non-coding sequences which typically evolve rapidly (LI *et al.*, 1985).

## DISCUSSION

Recently, we reported the results of experiments designed to investigate the relationship between thermal stability of DNA and the physical and chemical conditions experienced by hydrothermal vent organisms (DIXON *et al.*,

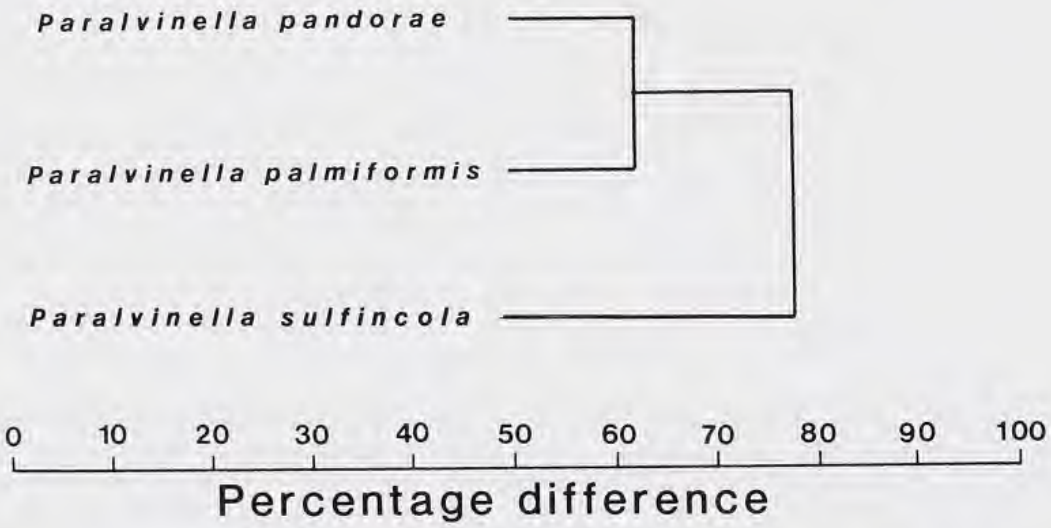



FIG. 4. — Unrooted tree based on percentage restriction-site differences between three species of *Paralvinella* from the Juan de Fuca Ridge.

Source : MNHN, Paris

1992). A positive correlation was found between the denaturing temperature of rDNA and environmental temperature for seven alvinellid species which was thought to be due to an increase in GC-content. In other organisms, increased GC-content has been shown to confer greater thermal and chemical stability to the DNA molecule (DARNELL *et al.*, 1986), and is an interesting molecular adaptation to hostile environmental conditions (e.g. BERNARDI & BERNARDI, 1990a, b). The results of the present investigation provide further evidence of increased GC-levels in the rDNA of some hydrothermal vent polychaetes and a shallow-water ampharetid, *M. palmata* (Table 1). The family Alvinellidae is closely related to, and perhaps derived from, the ampharetid polychaetes (DESBRUYÈRES & LAUBIER, 1986). The evidence presented here for increased GC-content in *M. palmata*, which tolerates highly-reduced and metal-rich sediments (GIBBS *et al.*, 1981), indicates that what may have arisen originally as an adaptation to harsh chemical conditions in shallow-water sediments, may have permitted colonisation of the high-temperature, and chemically hostile, hydrothermal vent environment in the distant past by a common ancestor (TUNNICLIFFE, 1992).

The topology of the unrooted tree shown in Figure 4 is divergent from present systematic relationships based on morphology which places *P. p. pandorae* as the most ancestral species of the genus. All other paralvinellid species have a different branchial form; among these species *P. palmiformis* and *P. sulfincola* form a sub-group with trifoliate tips on the buccal tentacles (DESBRUYÈRES & LAUBIER, 1991; TUNNICLIFFE *et al.*, 1993). A study of allozyme similarity among these species confirms the distance of *P. p. pandorae* but also makes a strong differentiation between *P. sulfincola* and *P. palmiformis* (D. JOLLIVET, pers. comm.). That morphological and molecular interpretations differ may be a function of the strong selection that is likely present on molecular functioning in an extreme habitat; morphological response may not be so strong. However, phylogenetic comparison of sequences that differ by more than 25 % is not recommended (UPHOLT, 1977); with greater differences there is increased probability that cleavage sites may be convergent (DOWLING *et al.*, 1990). The apparently high degree of divergence of these three species (up to 60 %) may reflect long evolutionary time, strong selection pressures, or both. While no certain fossil record is available, there are Cretaceous vent deposits with tubes reminiscent of those of Alvinella species (HAYMON & KOSKI, 1985); a large proportion of the vent fauna may be a Mesozoic relic (TUNNICLIFFE, 1992). High copy number sequences are generally not good candidates for constructing phylogenetic trees (HILLIS & MORITZ, 1990) and further work is required before good systematic relationships can be established among these species.

## ACKNOWLEDGEMENTS

The bulk of this work was funded by the UK Natural Environment Research Council through a rersearch grant to Prof. A.J. SOUTHWARD; VT was funded by NSERC Canada. Dr Peter HOLLAND (Oxford University) kindly donated several of the rDNA probes. We are grateful to David NICHOLSON for photographic assistance.

## REFERENCES

BERNARDI, G. & BERNARDI G., 1990a. — Compositional transitions in the nuclear genomes of cold-blooded vertebrates. *J. mol. Evol.*, **31** : 282-293.

BERNARDI, G. & BERNARDI G.,1990b. — Compositional patterns in the nuclear genomes of cold-blooded vertebrates. *J. mol. Evol.*, **31** : 265-281.

BROCK, T.D., 1985. — Life at high temperatures. *Science*, 230 : 132-138.

DARNELL, J., LODISH, H. & BALTIMORE, D., 1986. — *Molecular Cell Biology*. Scientific American Books, New York, 1192 pp.

DESBRUYÈRES, D. & LAUBIER, L., 1986. — Les Alvinellidae, une famille nouvelle d'annélides polychètes inféodées aux sources hydrothermales sous-marines : systématique, biologie et écologie. *Can. J. Zool.*, **64** : 2227-2245.

DESBRUYÈRES, D. & LAUBIER, L., 1991. — Systematics, phylogeny, ecology and distribution of Alvinellidae (Polychaeta) from deep-sea hydrothermal vents. *Ophelia Suppl.*, **5** : 31-45.

DIXON, D.R., SIMPSON-WHITE, R. & DIXON, L.R.J., 1992. — Evidence for thermal stability of ribosomal DNA sequences in hydrothermal-vent organisms. *J. mar. biol. Ass. U.K.*, **72** : 519-527.

Source : MNHN, Paris

DOWLING, T.E., MORITZ, C. & PALMER, J.D., 1990. — Restriction site analysis. *In*: D.M. HILLIS & C. MORITZ (eds), *Molecular Systematics*. Sinauer Associates Inc., Sunderland, Mass. : 250- 317.

GIBBS, P.E., BRYAN, G.W. & RYAN, K.P., 1981. — Copper accumulation by the polychaete *Melinna palmata*: an antipredation mechanism? *J. mar. biol. Ass. U.K.*, **61** : 707 - 722.

HAYMON, R.M. & KOSKI, R.A., 1985. — Evidence of an ancient hydrothermal vent community: fossil worm tubes in Cretaceaous sulfide deposit of the Samail Ophiolite, Oman. *Bull. Biol. Soc. Wash.*, **6** : 57-65.

HILLIS, D.M. & MORITZ, C., 1990. — *Molecular Systematics*. Sinauer Associates Inc., Sunderland, Mass., 588 pp.

HOLLAND, P.W.H., HACKER, A.M. & WILLIAMS, N.A., 1991. — A molecular analysis of the phylogenetic affinities of *Saccoglossus cambrensis* Brambell & Cole (Hemichordata). *Phil. Trans. R. Soc. Lond. B.*, **332** : 185-189.

KESSLER, C., HOLTKE, H.J., SEIBL, R., BURG, J. & MUHLEGGER, K., 1990. — Non-radioactive labelling and detection of nucleic acids: I. A novel DNA labelling and detection system based on digoxygenin: anti-digoxygenin ELISA principle. *Biol. Chem. Hoppe Seyler*, **371** : 917-927.

LI, W.-H., WU, C.-I. & LUO, C.-C., 1985. — A new method for estimating synonymous and nonsynonymous rates of nucleotide substitution considering the relative liklihood of nucleotide and codon changes. *Mol. Biol. Evol.*, **2** : 150- 174.

SAMBROOK, J., FRITSCH, E.F. & MANIATIS, T., 1989. — *Molecular cloning. A laboratory manual*, vol. 1, 2nd edition. Cold Spring Harbour Laboratory Press.

SCHMIDT, E.R., GODWIN, E. A., KEYL, H.-G. & ISRAELEWSKI, N., 1982. — Cloning and analysis of ribosomal DNA of *Chironomus thummi piger* and *Chironomus thummi thummi*. *Chromosoma* (Berlin), **87** : 389-407.

SOUTHERN, E., 1975. — Gel electrophoresis of restriction fragments. *Meth. Enzymol.*, **68** : 152-176.

TUNNICLIFFE, V., 1992. — The nature and origin of the modern hydrothermal vent fauna. *Palaios*, **7** : 338-350.

TUNNICLIFFE, V., JUNIPER, S.K. & de BURGH, M.E., 1985. — The hydrothermal vent community of Axial Seamount, Juan de Fuca Ridge. *Biol. Soc. Wash. Bull.*, **6** : 453-464.

TUNNICLIFFE, V., DESBRUYERES, D., JOLLIVET, D. & LAUBIER, L., 1993. — Systematic and ecological characteristics of *Paralvinella sulfincola* Desbruyères and Laubier, a new polychaete (family Alvinellidae) from Northeast Pacific hydrothermal vents. *Can. J. Zool.*, **71** : 286-297.

UPHOLT, W.B., 1977. — Estimation of DNA sequence divergence from comparison of restriction endonuclease digests. *Nucl. Acids. Res.*, **4** : 1257-1265.

Source : MNHN, Paris

# On the nature of the two anterior asetigerous rings in Dorvilleidae and Dinophilidae (Annelida, Polychaeta)

*Danny EIBYE-JACOBSEN*

Zoological Museum
Universitetsparken 15
DK-2100 Copenhagen Ø
Denmark

ABSTRACT

Members of the order Eunicida are apparently characteristic in possessing two more or less clearly separated rings between the prostomium and the first setiger. In the family Eunicidae it has previously been shown that these rings represent a subdivision of the peristomium related to the manner in which the longitudinal muscles are attached to the body wall. Nevertheless, this character may be a synapomorphy for Eunicida, provided that it is homologous among its members. This hypothesis is tested in members of the families Dorvilleidae and Dinophilidae through light microscopic studies of the body area in question. Recent publications have proposed that Dinophilidae is closely related to or actually a subtaxon of Dorvilleidae; this conclusion is not contradicted by the results of this investigation.

RÉSUMÉ

**Sur la nature des deux anneaux asétigères antérieurs réunis chez les Dorvilleidae et les Dinophilidae (Annelida Polychaeta)**

Les membres de l'ordre Eunicida paraissent caractérisés par la possession de deux anneaux plus ou moins nettement séparés entre le lobe céphalique et le premier sétigère. Pour la famille des Eunicidae on a démontré que ces anneaux représentent des subdivisions du péristomium en relation avec la manière par laquelle les muscles longitudinaux sont attachés aux parois du corps. Néanmoins, ce caractère peut être une synapomorphie pour les Eunicida, à condition qu'il soit homologue parmi ses membres. Cette hypothèse est mise à l'épreuve chez les membres des familles des Dorvilleidae et des Dinophilidae par des études microscopiques de cette région du corps. Dans des publications récentes, on a proposé que les Dinophilidae sont effectivement étroitement alliés à un sous-taxon des Dorvilleidae; cette conclusion n'est pas en contradiction avec les résultats de cette investigation.

## INTRODUCTION

In most members of the polychaete family Dorvilleidae the peristomium takes the form of two apodous rings between the prostomium and the first setiger. In most species these rings are subequal, but in many the anterior

EIBYE-JACOBSEN, D., 1994. — On the nature of the two anterior asetigerous rings in Dorvilleidae and Dinophilidae (Annelida, Polychaeta). *In*: J.-C. DAUVIN, L. LAUBIER et D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 93-100. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

one is shorter and indistinctly separated from the prostomium. Only few species show no trace of peristomial subdivision, e.g., four of the five hitherto described species of the genus *Exallopus* Jumars, 1974 (the exception is the type species, *E. cropion* Jumars, 1974). Some confusion has surrounded the nature of these two rings. Thus, while many authors have preferred neutral terms, such as rings, others appear to have regarded them as true segments (e.g., JIRKOV, 1989), where Dorvilleidae is characterized as having "two peristomial segments without parapodia, setae or cirri". The use of the word "segment" may in many instances have been coincidental, but in an evaluation of dorvilleid relationships with other polychaete groups it is important to understand the true nature of these rings. Within the order Eunicida conditions similar to those in Dorvilleidae are found in Eunicidae, Lumbrineridae (sensu ORENSANZ, 1990, including Lysaretidae), Hartmaniellidae, Oenonidae (= Arabellidae), and Iphitimidae (members of the families Histriobdellidae and Ichthyotomidae are too strongly modified to allow an assessment of this character). The major group in which only one peristomial ring is present is the family Onuphidae, which is considered the sister group of Eunicidae (ORENSANZ, 1990; FAUCHALD, 1992). Descriptions of the larval development of onuphids are not clear as to whether a peristomial subdivision is present during earlier stages in ontogeny (e.g., HSIEH & SIMON 1987 on *Kinbergonuphis simoni*). In his discussion of larval development in *Nothria elegans*, BLAKE (1975a) refers to the presence of such a subdivision but this is not confirmed by his illustrations.

The term peristomium, as it is currently used, is not applied to homologous structures in various polychaete families. In embryological terms, the peristomium has its origin in the region between the prototroch and the telotroch of the classical trochophora larva (e.g., GEORGE & HARTMANN-SCHRÖDER, 1985). This appears to be the case in Eunicida (see below). However, the adult peristomium of many polychaete families is a compound structure consisting of the peristomium s. str. as well as a variable number of anterior segments of teloblastic origin which have often lost their setae and parapodia and may possess paired tentacular cirri. Examples of these conditions may be seen in families such as Hesionidae, Syllidae, and Nereidae (GILPIN-BROWN, 1958).

For *Eunice kobiensis* (Eunicidae), ÅKESSON (1967a) gave a very convincing account of the embryological origin of the peristomium. According to his studies, the first setiger of adults corresponds to the first larval segment; the peristomium, including both rings and the peristomial cirri, must be interpreted as presegmental. ÅKESSON also provided an anatomical explanation for the strongly developed peristomial subdivision, which is found in this species. His studies showed that in the posterior region of the peristomium a number of fibres belonging to the ventral longitudinal muscle bands branch off in a lateral direction and attach themselves to the body wall at the level of the subdivision (ÅKESSON, 1967a: Fig. 11). In a similar manner, fibres of the dorsal longitudinal muscles give rise to the dorsal component of the visible, non-segmental furrow.

Assuming that the absence of any peristomial subdivision in Onuphidae may be regarded as a secondary phenomenon (possibly related to their being mostly tubicolous), the presence of two rings of true peristomial origin may be regarded as an autapomorphic character of Eunicida. Embryological observations indicate that ÅKESSON's observations on *Eunice* are valid for members of Dorvilleidae (e.g., ÅKESSON, 1967b, 1973a, and b on various species of *Ophryotrocha*; BLAKE, 1975b on *Dorvillea rudolphi*) in the sense that the two asetigerous rings are of peristomial origin. However, it remains to be demonstrated that a true homology exists, i.e., that a homologous pattern of muscle attachment is present.

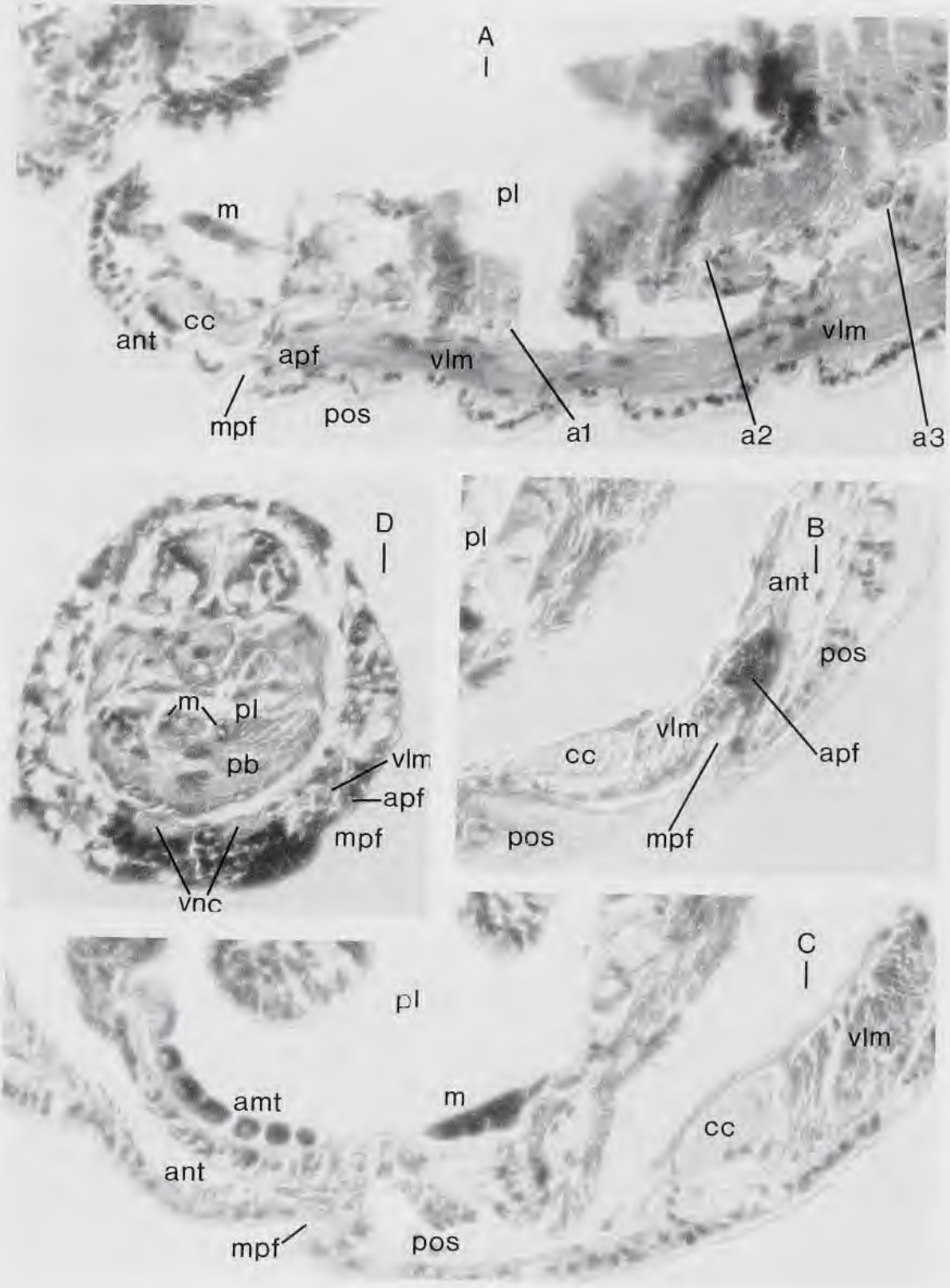
The primary purpose of this paper is to examine whether anatomical observations on various species of Dorvilleidae can confirm a homology on this point.

The family Dinophilidae was previously placed in Archiannelida, which was usually accorded order or class rank. In recent years, a body of evidence has grown that points to a close relationship between this family and Dorvilleidae (ÅKESSON, 1977; WESTHEIDE, 1985, 1987; ORENSANZ, 1990; EIBYE-JACOBSEN & KRISTENSEN, in press). However, since dinophilids are greatly reduced and highly specialized, much of the evidence is

---

FIG. 1. — A-C. *Protodorvillea kefersteini*, sagittal section showing ventrolateral longitudinal muscle band and attachment of accessory peristomial fibres to body wall at mid-peristomial furrow (A); cross section showing accessory peristomial fibres (in close proximity to ventrolateral longitudinal muscle band) attached to body wall (B); cross section 15-20 mm further posterior through anterior margin of mandible showing as yet undivided, strongly developed ventrolateral longitudinal muscle band (anterolateral, accessory mandibular teeth visible on left side) (C). D. *Ophryotrocha* cf. *hartmanni*, cross section, on right side corresponding to B (pharynx protruded). All scales = 10 mm. Nomarski differential interference contrast used on all figures. Abbreviations: a1 = aciculum of first setiger; a2 = aciculum of second setiger; a3 = aciculum of third setiger; amt = accessory mandibular teeth; ant = anterior peristomial ring (first post-prostomial ring); apf = accessory peristomial fibres; cc = circumesophageal connective; m = mandible; mpf = mid-peristomial furrow; ol = oesophageal lumen; pb = pharyngeal bulbus; pl = pharyngeal lumen; pos = posterior peristomial ring (second post-prostomial ring); vc = ventral ciliation; vlm = ventrolateral muscle band; vnc = ventral nerve cord.

Source : MNHN, Paris




Source : MNHN, Paris

circumstantial (larval resemblances, connections through theoretical morphological reduction series, parasite relationships; see above references for discussion). It has been difficult to find positive apomorphic characters that support a relationship. To date, the best such indication is the presence of an unpaired, pygidial stylus with a specific musculature in certain dorvilleid genera and most members of the dinophilid genus *Dinophilus* (WESTHEIDE, 1985).

There are difficulties in the homologisation of segments in dinophilids with those of other polychaetes, since parapodia and setae are absent. However, a peristomial subdivision resembling that in Dorvilleidae appears to be present, most clearly in the genus *Trilobodrilus*. The present study was in part undertaken to isolate yet another possible character to strengthen the view of a close relationship between these families (or at least, in the present context, the membership of Dinophilidae in Eunicida).

## MATERIALS AND METHODS

Several specimens of each of the following species were examined: *Protodorvillea kefersteini* (McIntosh, 1869); *Parougia eliasoni* (Oug, 1978); *Ophryotrocha* cf. *hartmanni* Huth, 1933; *O. puerilis siberti* (McIntosh, 1885); and *Trilobodrilus* cf. *nipponicus* Uchida & Okuda, 1943. The dorvilleid species were taken at various localities along the north coast of Brittany, France. The specimens of *Trilobodrilus* were found in samples of coarse sand and gravel taken off Ellekilde Hage in the southern Kattegat, Denmark.

The specimens were embedded in paraplast using standard techniques, sectioned to a thickness of 4 mm, and stained using a modification of Masson's trichrome method (Weigert's iron haemotoxylin, Ponceau's xylidine, and Fast Green). This renders muscle tissue bright red, whereas collagen and other connective structures are stained green. After dehydration, the sections were embedded in Entellan.

The sections were studied with a Leitz Ortholux microscope, whereas photographs were taken on a Zeiss Axiophot microscope, in most cases employing Nomarski differential interference contrast.

## RESULTS

*Protodorvillea kefersteini*

In the posterior part of the second asetigerous ring a group of muscle fibres (henceforth termed accessory peristomial fibres) leave the lateral part of each ventrolateral longitudinal muscle trunk (Fig. 1C). They attach to the body wall ventrolaterally on either side, midway along the length of the peristomium (Fig. 1B). Figure 1A shows a sagittal section in which a ventrolateral longitudinal muscle band is seen in the anterior setigers as well as the attachment of the accessory peristomial fibres to the body wall at the mid-peristomial furrow.

The ventrolateral longitudinal muscle trunks continue forward and insert on the body wall at the lower (posterior) lip of the mouth opening (not visible on Fig. 1A). These fibres may be confused with those of the anterior mandibular protractor muscles, which are also attached to the lower lip (DALES, 1962; not shown on ÅKESSON's (1967a) figures). However, the latter are inserted in a midventral position, whereas the paired ventrolateral longitudinal muscle trunks are ventrolaterally attached.

Accessory peristomial fibres also branch off from the dorsolateral longitudinal muscle trunks and are attached to the body wall further forward at the level of peristomial subdivision.

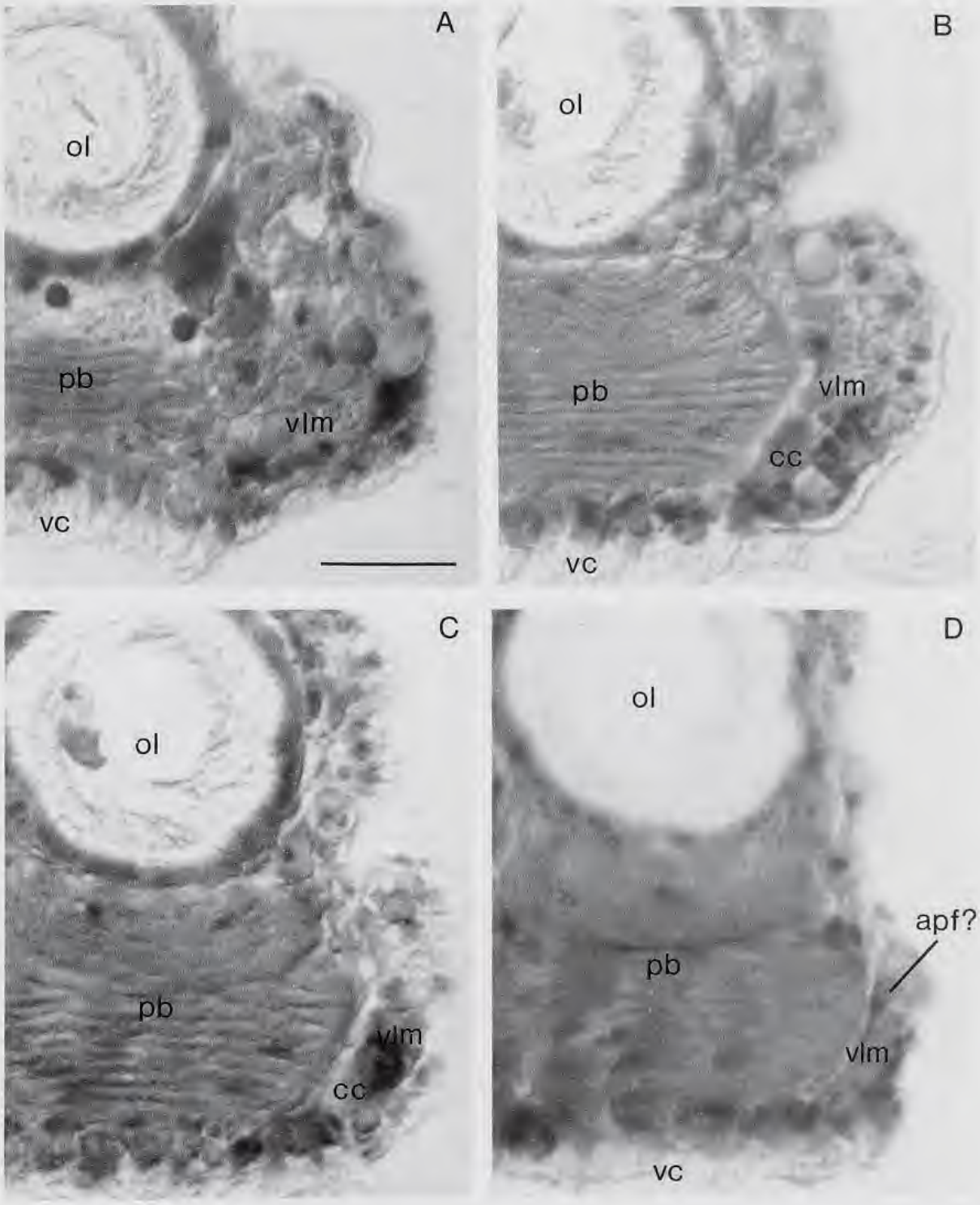
*Parougia eliasoni*

Observations on this species were identical to those described for *Protodorvillea kefersteini*.

---

FIG. 2. — *Trilobodrilus* cf. *nipponicus*, cross sections showing body becoming increasingly narrow in anterior portion of second post-prostomial ring, at narrowest point (D) showing subdivision of ventrolateral longitudinal muscle bundle, the dorsal component of which may be homologous to accessory peristomial fibres in Dorvilleidae. Scale A-D = 10 mm. Nomarski differential interference contrast used on A-C. Abbreviations: a1 = aciculum of first setiger; a2 = aciculum of second setiger; a3 = aciculum of third setiger; amt; = accessory mandibular teeth; ant = anterior peristomial ring (first post-prostomial ring); apf = accessory peristomial fibres; cc = circumesophageal connective; m = mandible; mpf = mid-peristomial furrow; ol = oesophageal lumen; pb = pharyngeal bulbus; pl = pharyngeal lumen; pos = posterior peristomial ring (second post-prostomial ring); vc = ventral ciliation; vlm = ventrolateral muscle band; vnc = ventral nerve cord.

Source : MNHN, Paris




Source : MNHN, Paris

*Ophryotrocha* cf. *hartmanni*

The sectioned material of this species, although of a poorer quality, shows the presence of accessory peristomial fibres (Fig. 1D) attaching to the body wall at the level of the mid-peristomial furrow. As in the other dorvilleids that were examined, the accessory fibres branch off from the ventrolateral muscle bands in the posterior part of the second peristomial ring. The animal shown was fixed with the pharynx somewhat protruded; the accessory peristomial fibres are contracted and therefore the two posterior mandibular rods are visible. It was not possible to observe whether dorsal accessory fibres are present.

*Ophryotrocha puerilis siberti*

Observations on this species were as described for *O.* cf. *hartmanni*.

*Trilobodrilus* cf. *nipponicus*

From the middle of the second post-prostomial ring (Fig. 2A) to the furrow between the first and second rings (Fig. 2D) body width decreases from 54 mm to 38 mm. Observations on the possible presence of accessory peristomial fibres was hampered by the small size of the animals in question. Thus, in any given cross section each ventrolateral muscle band consists of 2-4 cells only. However, at the level of the furrow between the first two post-prostomial rings, the dorsalmost of these cells appears separated from the others. It was not possible to observe whether it was attached to the body wall at this point, but this cell is absent on more anterior sections, indicating that its rostral end must be very close to the furrow.

## DISCUSSION

In the dorvilleid species studied, subdivision of the peristomium appears to be induced (at least in part) by the attachment of accessory muscle fibres with an origin in the longitudinal trunks. These observations correspond to those reported by ÅKESSON (1967a) for *Eunice kobiensis*, the only important difference being that the accessory fibres remain close to the main trunk throughout their entire length. In *Eunice* (as indicated on ÅKESSON's drawing) the ventral accessory peristormial fibres and the ventrolateral muscle bands appear to be clearly separated rostrally. This disparity may be due to differences in degree of muscle contraction.

Recently, ORENSANZ (1990) has suggested that a number of dorvilleid genera, among them *Ophryotrocha* should be placed in the family Iphitimidae. Doubtless a close relationship between Dorvilleidae and Iphitimidae exists. However, as the character studied in the present paper is most likely common to the entire order Eunicida, it probably has no bearing on inter-familial relationships. The question of whether ORENSANZ' rearrangement of genera is justified will be treated in a separate paper (EIBYE-JACOBSEN & KRISTENSEN, in press).

The accessory peristomial fibres and thus the subdivision of the peristomium in Dorvilleidae are very probably homologous to those in Eunicidae. Although corresponding anatomical studies have not yet been carried out on members of families such as Lumbrineridae and Oenonidae, and disregarding the aberrant conditions in Onuphidae, the presence of a secondary peristomial subdivision in association with a specific pattern of muscle attachment appears to be an autapomorphic character for the order Eunicida. Even though external signs of genuine peristomial subdivision are lacking in other polychaete groups, it would be preferable to test this hypothesis by carrying out corresponding studies on some of them. The sister group of Eunicida would be of special interest. Unfortunately, it is at the present time difficult to form an informed opinion as to which polychaete groups are likely candidates, as Eunicida is generally considered a somewhat isolated group (DALES, 1962; STORCH, 1968; FAUCHALD, 1977).

On the basis of the present study of *Trilobodrilus*, it is neither possible to conclude that accessory peristomial fibre(s) exist nor that the two anterior post-prostomial rings represent a subdivided peristomium. The results are too uncertain and the apparent presence of a muscle cell disassociated from the others of the ventrolateral longitudinal muscle band (Fig. 2D) may be due to an artifact. The fact that this cell has a dorsolateral position relative to the longitudinal muscle band (lateral in Dorvilleidae, ventrolateral in Eunicidae) should not be seen as a hindrance to considering the phenomenon (if it exists) as homologous. In all cases, the fibres that branch off are the most lateral ones and it is the orientation of the longitudinal muscle bands which varies. Ultrastructural studies must, however, be carried out before it can confidently be concluded that a homology does exist on this point between dinophilids and eunicidans.

ÅKESSON (1967a) and subsequently other authors have suggested that the function of the accessory peristomial fibres is to augment the operation of the complicated jaw apparatus present in members of the order Eunicida. No

Source : MNHN, Paris

actual mechanism for this has been proposed. In *Ougia subaequalis* (OUG, 1978) the pharynx may reach into setiger 13 with the maxillae placed in setiger 6 in the retracted state. In many other dorvilleids some of the anterior setigers also house parts of the pharyngeal apparatus. Thus, although the division of the peristomium may originally have had an explanation in accordance with ÅKESSON's hypothesis, it is difficult in light of their dimensions to credit the accessory peristomial fibres with an important role during pharyngeal protraction in all dorvilleid species.

Certainly, if it were later to be demonstrated that accessory peristomial fibres are present in dinophilids they must be regarded as rudiments or have some other function, as they are completely dwarfed by the strongly developed pharyngeal bulb (Fig. 2D).

## ACKNOWLEDGMENTS

I wish to thank Wilfried WESTHEIDE (University of Osnabrück, Germany) for suggesting this line of investigation and for being a generous host during an extended visit to his institute. The assistance of the staff at the Station Biologique (Roscoff, France), especially that of Captain Alain MARON, during the collection of most of the animals used in this study is greatly appreciated. Kurt OCKELMANN (Marine Biological Laboratory, Helsingør, Denmark) kindly furnished the specimens of *Trilobodrilus*. Margit JENSEN (Zoological Museum, University of Copenhagen) is thanked for the use of her Zeiss Axiophot microscope (Carlsbergfondet grant no. 468). The Danish Natural Science Research Council provided post-doc funding for this project (grant no. 11-8808).

## REFERENCES

ÅKESSON, B., 1967a. — The embryology of the polychaete *Eunice kobiensis*. *Acta Zool.*, **48** : 141-192.

ÅKESSON, B., 1967b. — On the biology and larval morphology of *Ophryotrocha puerilis* Claparède & Metschnikov (Polychaeta). *Ophelia*, **4** : 111-119.

ÅKESSON, B., 1973a. — Morphology and life history of *Ophryotrocha maculata* sp. n. (Polychaeta, Dorvilleidae). *Zoologica Scr.*, **2** : 141-144.

ÅKESSON, B., 1973b. — Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). *Zoologica Scr.*, **2** : 145-155.

ÅKESSON, B., 1977. — Parasite-host relationships and phylogenetic systematics. The taxonomic position of Dinophilids. *Mikrof. Meeresb.*, **61** : 19-28.

BLAKE, J.A., 1975a. — The larval development of Polychaeta from the northern California coast. II. *Nothria elegans* (family Onuphidae). *Ophelia*, **13** : 43-61.

BLAKE, J.A., 1975b. — The larval development of Polychaeta from the northern California coast. III. Eighteen species of Errantia. *Ophelia*, **14** : 23-84.

DALES, R.P., 1962. — The polychaete stomodeum and the inter-relationships of the families of Polychaeta. *Proc. Zool. Soc. Lond.*, **139**: 389-428.

EIBYE-JACOBSEN, D. & KRISTENSEN, R.M. (in press). — The description of a new genus and species of Dorvilleidae (Annelida: Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Dinophilidae, and Iphitimidae. *Zool. Scr.*

FAUCHALD, K., 1977. — The Polychaete Worms. Definitions and keys to the orders, families and genera. *Nat. Hist. Mus. Los Angeles County, Sci. Ser.*, **28** : 1-190.

FAUCHALD, K., 1992. — A review of the genus *Eunice* (Polychaeta: Eunicidae) based upon type material. *Smithson. Contrib. Zool.*, **523** : 1-422.

GEORGE, J.D. & HARTMANN-SCHRÖDER, G., 1985. — Polychaetes: British Amphinomida, Spintherida and Eunicida. *Synop. Brit. Fauna*, **32** : 1-221.

GILPIN-BROWN, J.B., 1958. — The development and structure of the cephalic nerves in *Nereis*. *J. Comp. Neurol.*, **109** : 317-348.

HSIEH, H.-L. & SIMON, J.L., 1987. — Larval development of *Kinbergonuphis simoni*, with a summary of developmental patterns in the family Onuphidae (Polychaeta). *Biol. Soc. Wash. Bull.*, **7** : 194-210.

Source : MNHN, Paris

JIRKOV, I.A., 1989. — *The bottom fauna of the seas of the USSR. Polychaetes.* (In Russian). Moscow State University, 140 pp.

ORENSANZ, J., 1990. — The Eunicemorph polychaete annelids from Antarctic and Subantarctic seas with addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the southern Indian Ocean. *Biol. Antarc. Seas*, **21** : 1-183.

OUG, E., 1978. — New and lesser known Dorvilleidae (Annelida, Polychaeta) from Scandinavian and northeast American waters. *Sarsia*, **63** : 285-303.

STORCH, V., 1968. — Zur vergleichenden Anatomie der segmentalen Muskelsysteme und zur Verwandtschaft der Polychaeten-Familien. *Z. Morph. Tiere*, **63** : 251-342.

WESTHEIDE, W., 1985. — The systematic position of the Dinophilidae and the archiannelid problem. *In* : S.C. MORRIS, J.D. GEORGE, R.GIBSON & H.M. PLATT (eds), *The Origins and Relationships of Lower Invertebrates*, **28** : 310-326. The Systematics Association, Oxford.

WESTHEIDE, W., 1987. — Progenesis as a principle in meiofauna evolution. *J. Nat. Hist.*, **21** : 843-854.

Source : MNHN, Paris

# The head of Maldanidae polychaetes of the subfamily Maldaninae

*Karen D. GREEN*

1537 Camino Corto
Fallbrook, CA, 92028, USA

ABSTRACT

The Maldaninae head and proboscis are described based on dissections of *Asychis amphiglyptus*, *Bathyasychis cristatus*, *Chirimia lobata*, *Maldane sarsi*, *Metasychis disparidentatus*, *Sabaco elongatus*, and *Sonatsa meridionalis*. Consistent features among these species include a well-developed cephalic plate with the rim divided by lateral notches, a wide and muscular palpode, a tri-lobed mouth, and an asymmetrical proboscis. It is suggested that the feeding structure is an axially-modified ventral proboscis. Variable features include the development of the cephalic rim, nuchal organs, palpode, mid-dorsal keel, and proboscis muscles.

RÉSUMÉ

**La tête des polychètes Madanidae de la sous-famille des Maldaninae**

La description de la tête et du proboscis de *Asychis amphiglyptus*, *Bathyasychis cristatus*, *Chirimia lobata*, *Maldane sarsi*, *Metasychis disparidentatus*, *Sabaco elongatus* et *Sonatsa meridionalis* a été effectuée à partir de dissections. Les principales caractéristiques chez ces espèces sont la présence d'une plaque céphalique bien développée avec un limbe divisé par des échancrures latérales, un palpode large et musculaire, une bouche trilobée, et un proboscis asymétrique. Il est suggéré que cette structure pour l'alimentation provient d'un proboscis ventral axial modifié. Des caractéristiques variables ont été observées sur le développement du limbe céphalique, les organes nucaux, le palpode, la carène médio-dorsale et les muscles du proboscis.

## INTRODUCTION

The head is a key feature in the taxonomy of Maldanidae polychaetes. The subfamily Maldaninae (ARWIDSSON, 1907; LIGHT, 1991) is characterized as having a cephalic plate, which refers to the dorsal surface of the head being edged by a raised rim. The cephalic rim is divided by lateral notches into a single posterior border and paired lateral borders. The prostomial palpode is anterior to the plate. Paired nuchal organs occur on the dorsal surface of the plate immediately behind the palpode. A keel (= carina, internuchal ridge, median ridge) refers to a medially raised area between the nuchal organs that may or may not extend into the posterior cephalic border.

Historically, the height and length of the keel was used in keys to separate the Maldaninae genera *Asychis* and *Maldane* (e.g., ARWIDSSON, 1907; FAUCHALD, 1977). However, interpretation of whether the keel is short and

GREEN, K.D., 1994. — The head of Maldanidae polychaetes of the subfamily Maldaninae. *In:* J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 101-109. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

low, or long and high may be difficult (FAUCHALD, 1972: note, keel referred to as palpode). In his revision of the Maldaninae, LIGHT (1991) considered other head features to be of generic importance; i.e., palpode shape, nuchal organ shape, and the development and shape of the lateral borders of the cephalic rim (= lobes, margins) including the degree offusion or separation of them from the palpode.

In contrast to the above features, the mouth and proboscis have received little attention. ARWIDSSON (1907) characterized the maldanin proboscis as being fairly uniform in width, but with a short plate-like bladder at the base, and lacking papillae. ORRHAGE (1973) histologically examined the foregut of *Asychis biceps* and characterized it as a cuticularized ventral sac (with an underlying muscle bulb) beneath a ciliated esophagus. He considered these features to be consistent with DALES (1962) ventral proboscis category.

Muscles concerned with the operation of the maldanin proboscis have not been described. The only available information concerns the maldanid subfamily Euclymeninae (PILGRIM, 1966; KUDENOV, 1977), which have an axial proboscis (ULLMAN & BOOKHOUT, 1949; DALES, 1962; PILGRIM, 1966; ORRHAGE, 1973; KUDENOV, 1977; TZETLIN, 1991). In euclymenins, two paired groups of muscles function as proboscis retractors. The largest set includes the retractor sheath, which inserts on the cuticularized buccal area; and the gular membrane, which inserts on the ciliated esophageal area (sometimes referred to as pharynx). The retractor sheath and gular membrane are considered derivatives of a single septum; their origin on the ventrum marks the boundary between the head and thorax (PILGRIM, 1966). The smallest set of muscles, termed the accessory buccal retractors, insert on the anterior portion of the buccal region (KUDENOV, 1977; PILGRIM, 1966).

The purpose of this paper is to provide additional information about the maldanin head and to describe the foregut and its musculature. Consistency and variability of head features within the subfamily are addressed by examination of representatives of Maldaninae genera recognized by GREEN (1987) and LIGHT (1991): *Asychis*, *Chirimia*, *Maldane*, *Metasychis*, *Sabaco*, and *Sonatsa*.

## MATERIALS AND METHODS

Non-type specimens were examined from the Allan Hancock Foundation (AHF) in cooperation with the Los Angeles County Museum of Natural History, and from the author's collection. Material included: *Asychis amphiglyptus*, Antarctica, Hope Bay, 3.5-7.5 m, Staten Island station 46-63 (original label as *Maldane sarsi*) (AHF); *Bathyasychis cristatus*, South America, Peru-Chile Trench, 8°43'S, 80°40'W, 3,939 m, Anton Bruun station AB11-168 (original label as *Sonatsa meridionalis*) (AHF); *Chirimia lobata*: Southern California, San Diego Trough, 32°25'-26°0'N, 117°26.8'-117°28.1'W, 1208-1244 m, trawl, Rokop station 71-45 (original label as *Asychis lobata*) (AHF); *Maldane sarsi*, Arctic Alaska, 71°09.8'N, 151°09.3'W, 45 m (donated by H. JONES); *Maldane* cf. *sarsi*, southern California, Santa Monica Bay, 184 m (donated by L. HARRIS); *Metasychis disparidentatus*, southern California, Newport Beach, 100 m (donated by L. LOVELL); *Sabaco elongatus*, northern California, San Francisco Bay (donated by M. WICKSTEN); *Sonatsa meridionalis*, South America, Peru-Chile Trench, 8°38'S, 80°40'W, 3,590-3,479 m, trawl, Anton Bruun station AB11-165 (AHF). Representatives of all examined species are retained in the AHF.

Terminology used by PILGRIM (1966) and KUDENOV (1977) to describe heads of euclymenins is largely adopted. However, their use of the term pharynx for the ciliated portion of the proboscis is not followed. This is because the term pharynx has been variously defined as a muscular portion of the proboscis (DALES, 1962) or as the entire stomodeal region involved in the uptake of food (PURSCHKE, 1988). Here, the proboscis is considered the protrusile part of the gut; I refer to the cuticularized portion as the buccal mass, and the ciliated portion as the esophagus.

Nuchal organ shape is described with reference to stems and tips. The stem is the end most posterior on the head; the tip is anterior. In the case of recurved nuchal organs, the stem is alongside the internuchal area, and the tip curves away.

Internal features were studied through dissections; a sagittal cut was made through the head and at least the first setiger. Drawings were made using a drawing tube fitted to a dissecting microscope. The surface of the foregut was characterized as cuticularized (i.e., same appearance as the external integument) or ciliated (i.e., finely textured or granular appearance). The presence or absence of cilia was confirmed by examining slide preparations of each type of surface using a compound microscope.

Features identified in the figures are abbreviated, as follows:

A = aboral annulus; ABR = accessory buccal retractors; BM = buccal mass; B.H/T = boundary of head and

Source : MNHN, Paris

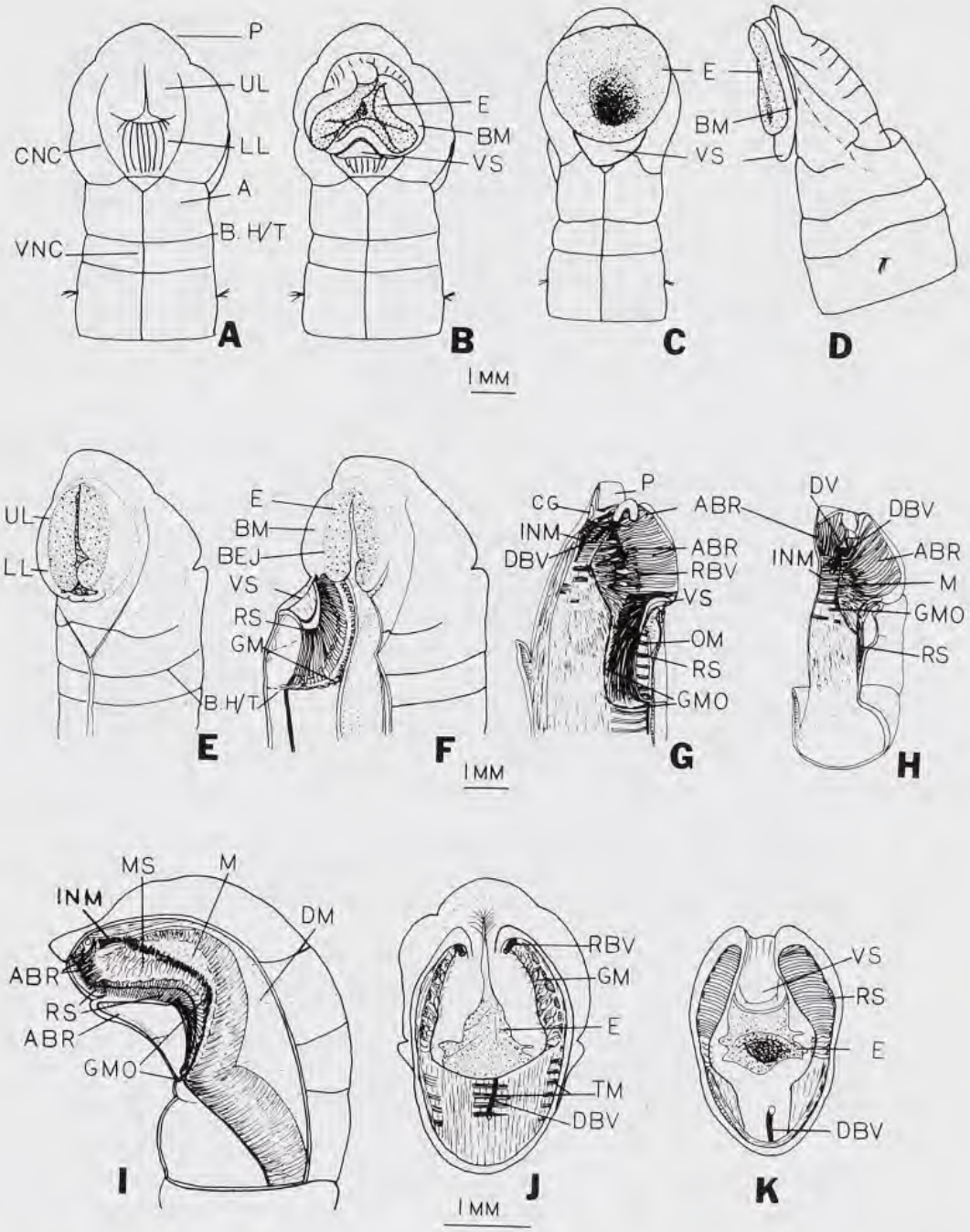



FIG. 1. — *Maldane* cf. *sarsi*: A, ventral view of head and first thoracic segment; B, ventral view, proboscis partially retracted; C, ventral view, proboscis everted; D, lateral view, proboscis everted. *Asychis amphiglyptus*: E, ventro-lateral view, proboscis partially everted; F, same view as in E, but with mid-ventral cut and right side folded back; G, internal ventro-lateral view with esophageal portion of proboscis removed; H, ventral view of G. *Maldane sarsi*: I, lateral view with foregut and musculature exposed; J, ventral view of transverse cut made dorsal to retractor sheath; K, dorsal view of head exposed from transverse cut in J. Note: not all blood vessels are shown. See Materials and Methods for definition of letter abbreviations.

Source : MNHN, Paris

thorax; BEJ = bucco-esophageal junction; CG = cerebral ganglion; CM = circular muscle; CNC = circumesophageal nerve connective; DBV = dorsal blood vessel; DM = dorsal mesentery; DV = dorsal valve; E = esophagus; GM = gular membrane; GMO = gular membrane origin; INM = internuchal muscle; K = keel; LL = lower lip; LB = lateral border; LM = longitudinal muscle; OM = oblique muscle; M = membrane; MS = muscle strands; NO = nuchal organs; P = palpode; PB = posterior border; POC = paroesophageal cavity; RBV = retractor blood vessel; RS = retractor sheath; SP = septum; TM = transverse muscle; UL = upper lip; VBV = ventral blood vessel; VNC = ventral nerve cord; VS = ventral sac.

## RESULTS

*Head/Thorax Boundary.* The head extends from the prostomial palpode to the first complete annulus (Fig. 1A-D), which includes the ventral origin of the retractor sheath and gular membrane (Fig. 1E). The prostomial palpode is fused to the peristomium, which is ventrally biannulate. A ventro-lateral groove, anterior to the bifurcation of the nerve cord, separates the mouth from an aboral annulus (Fig. 1A). The first complete annulus and the following setous one form the first biannulate thoracic segment, whose posterior boundary is marked by a septum (e.g., Fig. 2B).

*Cephalic Rim.* The cephalic plate has smooth borders in most of the examined species, but they are serrate in Chirimia lobata and Metasychis disparidentatus (Fig. 2, dorsal views). The transition between the palpode and lateral margins is gradual in *Sonatsa elongatus*, marked by shallow notches in *Asychis amphiglyptus*, *Bathyasychis cristatus* and *Maldane sarsi*, or marked by clefts in *Chirimia lobata* and *Metasychis disparidentatus*.

*Palpode.* The palpode is as wide or wider than the mouth in all examined specimens (e.g., Fig 1A). The shape of the palpode complements the shape of the plate (Fig. 2, top views). That is, the palpode is rounded and nearly the same width of the rounded plate in *Asychis amphiglyptus*, *Bathyasychis cristatus*, *Chirimia lobata*, and *Sabaco elongatus*. In contrast, the palpode is spade-shaped and less than 75 % the width of the elongate plate in *Metasychis disparidentatus*, *Maldane sarsi*, and *Sonatsa meridionalis*. The palpode is upturned in *Chirimia lobata*, conical in *Sonatsa meridionalis*, and angular in profile in the other species. The palpode is muscular (Fig. 2, sagittal views); transverse muscle development is greatest in *Sonatsa meridionalis* (Fig. 2B).

*Nuchal Organs.* The nuchal organs differ in shape and length (Fig. 2, top views). Nuchal organs with nearly parallel stems have tips that diverge or slightly curve as in *Maldane sarsi* (Fig. 2A), strongly curve or bend laterally as in *Asychis amphiglyptus* and *Metasychis disparidentatus* (Fig. 2D,F), or recurve as in *Chirimia lobata* and *Sabaco elongatus* (Fig. 2C,G). Stems curve laterally and tips are nearly parallel in *Sonatsa meridionalis* (Fig. 2B). The stems and tips both diverge in *Bathyasychis cristatus* (Fig. 2E). Nuchal organs are reduced (< 1/6 head length) in *Sabaco elongatus*; short (1/6 to 1/3 head length) in *Bathyasychis cristatus*, *Metasychis disparidentatus*, *Maldane sarsi*, and *Sonatsa meridionalis*; and of moderate length (1/3 to 1/2 head length) in *Asychis amphiglyptus* and *Chirimia lobata*.

Behind the cerebral ganglion and beneath the nuchal organs is a concentration of transversely oriented muscle bundles, herein termed the internuchal muscle (Fig. 2, sagittal views). This muscle is least developed in *Sabaco elongatus* (Fig. 2C) and most developed in *Chirimia lobata* (Fig. 2G). The length of the internuchal muscle approximates that of the nuchal organs in *Bathyasychis cristatus*, *Maldane sarsi*, and *Sabaco elongatus*; the nuchal organs are slightly longer than the internuchal muscle in *Asychis amphiglyptus*, *Chirimia lobata*, and *Metasychis disparidentatus*. Keel development obscures the dorsal boundary of the internuchal muscle in Sonatsa meridionalis (Fig. 2B).

*Keel.* The keel is convex, long, narrow, and firm in *Maldane sarsi* and *Sonatsa meridionalis* (Figs. 2A,B). These keels are supported by multiple layers of transverse muscle bundles that extend from the palpode to the posterior border of the plate. However, thedevelopment of the keel muscle differs between these species. The transverse muscle bundles are interspersed within a dense layer of longitudinal muscle in *Maldane sarsi*. In contrast, dense aggregations of transverse muscle occur below a layer of longitudinal muscle in *Sonatsa meridionalis*.

Most of the other species have slightly convex (*Metasychis disparidentatus* and *Sabaco elongatus*) to flat (*Asychis amphiglyptus* and *Chirimia lobata*) keels that are marked by a single layer of transverse muscle bundles, the extent of which corresponds to keel length. These keel are relatively narrow and compressible (loses shape when pressed). The keel is relatively wide and firm in *Bathyasychis cristatus* (Fig. 2E). The firmness probably reflects a bulging of the proboscis; there is little space between the esophagus and the inner wall of the head.

*Mouth.* All examined specimens have a transverse opening and a medially incised upper lip; the lower lip has

Source : MNHN, Paris

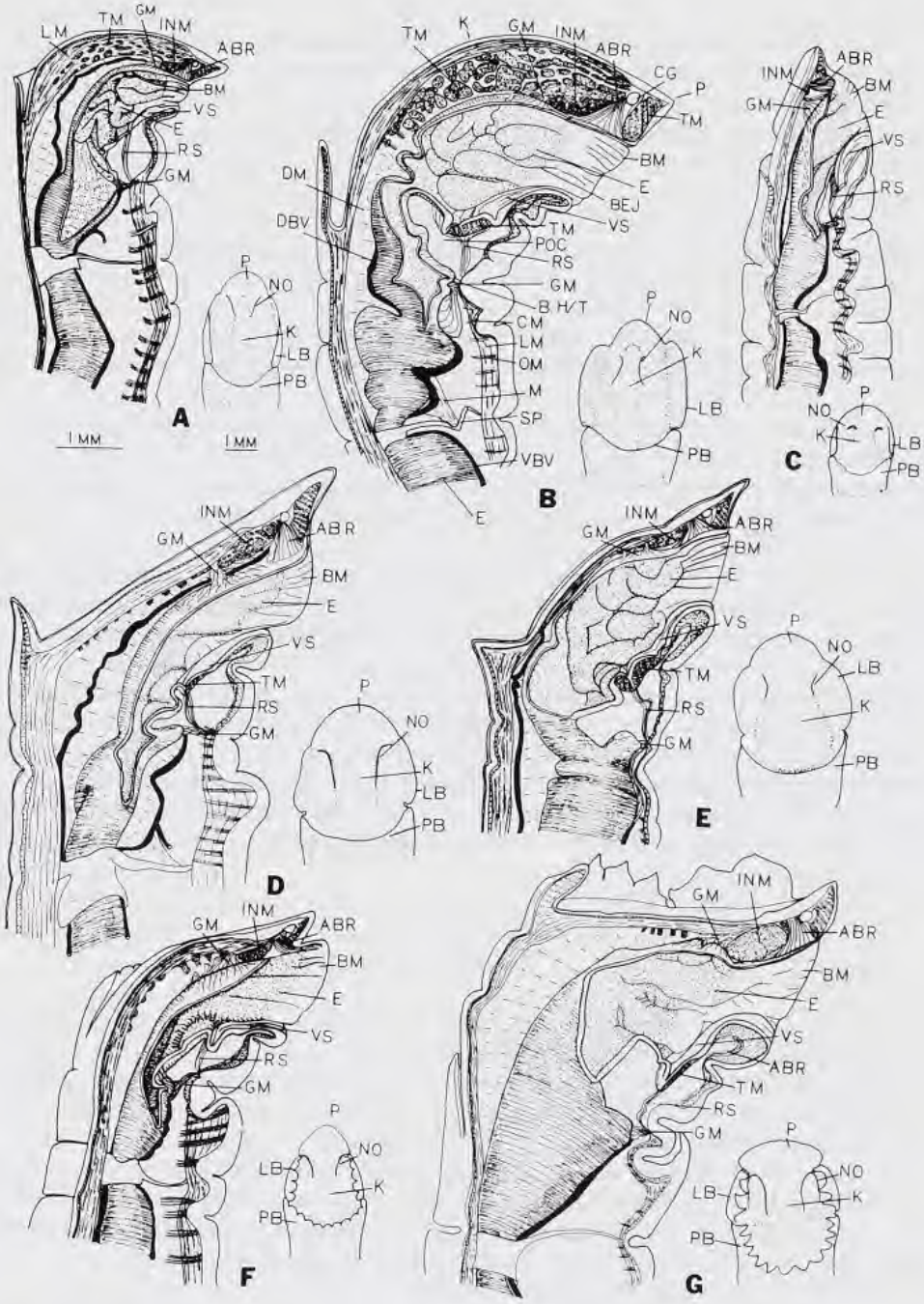



FIG. 2. — Sagittal and dorsal views of heads: A, *Maldane sarsi*; B, *Sonatsa meridionalis*; C, *Sabaco elongatus*; D, *Asychis amphiglyptus*; E, *Bathyasychis cristatus*; F, *Metasychis disparidentatus*; G, *Chirimia lobata*. Notes: All sagittal and dorsal views, respectively, drawn at same scale; scale for each view shown in Fig. 2A. Equivalent features in all sagittal views have same shading pattern, see Fig. 2B for detailed labeling. Not all blood vessels and oblique muscles are shown. See Materials and Methods for definition of letter abbreviations.

Source : MNHN, Paris

several longitudinal folds (e.g., Fig. 1A).

*Proboscis*. Of the examined material, one specimen of *Maldane* has a fully everted proboscis (Fig. 1C-D), and one specimen of *Asychis* has a partially everted proboscis (Fig. 1E-F). The proboscis consists of a cuticularized buccal mass and the anterior part of the ciliated esophagus. The everted part of the esophagus is cushion-shaped; the everted buccal region is asymmetrical with abasal extension (herein termed ventral sac).

In the retracted state, the proboscis is similar among the examined species (Fig. 2, sagittal views). The cuticularized region is smooth and slightly folded. Part of it extends from the edges of the upper lips to the esophagus. Another part infolds from the corner of the mouth and forms the ventral sac below the esophagus (Fig. 1J-K; Fig. 2, sagittal views).

Transverse muscle may occur beneath the retracted ventral sac. This muscle is relatively well-developed in Bathyasychis cristatus and *Sonatsa meridionalis* (Figs. 2B,E), is present in *Asychis amphiglyptus* and *Chirimia lobata* (Figs. 2D,G), and is reduced in *Metasychis disparidentatus*, *Maldane sarsi*, and *Sabaco elongatus* (Figs. 2A,C,F).

The proboscides also differ with regard to how folded the esophagus is when retracted. The folds are taken here as an indication of proboscis volume; given this, the largest volume proboscides were noted for *Bathyasychis* and *Sonatsa*.

*Proboscis Retractors*. On each side of the head, the gular membrane and retractor sheath originate along a path from the head/thorax boundary towards the level of the lateral notches (Fig. 1G-I). From there, the origin of the gular membrane continues dorsally and anteriorly to the end of the plate. The retractor sheath divergesventrally. Accessory buccal retractors originate behind the cerebral ganglion and along the line of the circumesophageal nerve connectives.

Along the origin of the gular membrane, muscular strands extend ventro-laterally (anterior face) and a thin membrane extends dorso-laterally (posterior face) (Fig. 1I). The muscular part of the origin ends behind the internuchal muscle; the membranous part continues anteriorly beneath the internuchal muscle to the dorsal valve (Fig. 1H-I). The gular membrane inserts on the ciliated esophagus.

This is reversed for the retractor sheath, which has muscular strands on the posterior face and a thin membrane on the anterior face (ventro-lateral). The retractor sheath inserts on the cuticularized ventral sac and the line of insertion continues towards the posterior corner of the upper lip (Fig. 1I).

Accessory buccal retractors lack an obvious membranous sheet, and the muscle strands insert on the buccal mass nearest the mouth. They are most developed dorso-laterally, and slightly overlap the retractor sheath near the corner of the mouth. Ventrally, they are less developed; they insert on the ventral buccal mass, but were not observed where the retractor sheet inserts.

## DISCUSSION

Maldaninae is one of the seven subfamilies of Maldanidae: Clymenurinae, Euclymeninae, Lumbriclymeninae, Maldaninae, Nicomachinae, Notoproctinae, and Rhodininae (ARWIDSSON, 1907; DETINOVA, 1985a; IMAJIMA & SHIRAKI, 1982). Most subfamilies were established on the basis of the head and pygidial regions and setal structure, although glands were used to establish Clymenurinae (IMAJIMA & SHIRAKI, 1982). The key head feature has been whether or not the head is modified as a plate.

Results suggest additional head features that may be useful at the subfamily level. The examined specimens shared the following features in common. The head includes a fused prostomium and peristomium, and the peristomium is biannulate. The palpode is muscular and at least as wide as the mouth. The mouth is trilobed with a transverse fissure and medially incised upper lip. Further, all species have an asymmetrical axially-modified ventral proboscis. These features are discussed further below.

The composition of the maldanid head has been controversial, but it is agreed that the prostomium and peristomium are fused (PILGRIM, 1966; LIGHT, 1991). PILGRIM (1966) considered the peristomium of some euclymenins to include an additional fused segment based on the ventral accessory buccal retractors' origin, which she associated with an aboral groove on the ventrum. In maldanins, the ventral origin of these muscles is associated with the nerve connectives rather than the aboral groove. Further, the line oforigin is interrupted by the retractor sheath, and the accessory retractors lack an obvious membrane. For these reasons, I interpret the aboral groove as indicative of a biannulate peristomium rather than a septum.

Palpode development and mouth shape need further assessment in maldanids. Instead of a wide muscular palpode, as in maldanins, some euclymenins have a muscular palpode that is narrower than the mouth (PILGRIM,

Source : MNHN, Paris

1966). However, information about the extent and musculature of the prostomial palpode is lacking for most maldanids. Narrow palpodes are common in clymenurins and euclymenins, and indistinct palpodes are common in the other subfamilies (IMAJIMA & SHIRAKI, 1982). A tri-lobed mouth, as in maldanins, may be unique. Other maldanids have a transverse or longitudinal fissure (IMAJIMA & SHIRAKI, 1982; KUDENOV, 1977; PILGRIM, 1966; TZETLIN, 1991); however, since mouths are rarely mentioned, this feature needs additional study.

Maldanin proboscides appear to differ from the few available reports for other maldanids. ORRHAGE (1973) characterized *Asychis biceps* as having a ventral proboscis because a cuticularized ventral sac (with an underlying muscle bulb) occurs below the ciliated esophagus. He stated that the ventral sac and muscle bulb were less voluminous in this species than in other species with ventral proboscides; i.e., *Nicomache lumbricalis* (Nicomachinae) and *Rhodine gracilior* (Rhodininae), but further detail was not given.Results indicate that the ventral sac is common in maldanins, but the development of the underlying transverse muscle (bulb) is variable. Based on TZETLIN's (1991) illustrations of *Nicomache lumbricalis*, *Nicomache minor*, and *Praxillura longissima* (Lumbriclymeninae), my impression is that the muscle bulb (ventral pharyngeal organ) is less developed in maldanins. Further the configuration of the maldanin proboscis differs from the ventral proboscides of *Nicomache minor* and *Praxillura longissima*. In those species, the non-ciliated region primarily is a ventral structure and the ciliated region primarily is dorso-lateral. In contrast, the non-ciliated region of the foregut is developed both dorsally and ventrally in maldanins, but it forms a narrow sac ventrally.

Because the non-ciliated and ciliated regions evert as a tube-like structure in maldanins, there is some similarity to the axial proboscides of euclymenins (DALES, 1962; PILGRIM, 1966; KUDENOV, 1977; TZETLIN, 1991). However, the ventral sac at the base of the maldanin proboscis gives it an asymmetrical appearance. This difference in the ventral development of the proboscis is reflected in the proboscis musculature. In euclymenins, the gular membrane and retractor sheath share the same origin (PILGRIM, 1966; KUDENOV, 1977). In maldanins, the retractor sheath diverges and follows a more ventral course. Further, accessory buccal retractors, which are well-developed in euclymenins, are mainly dorso-lateral in maldanins and only weakly developed ventrally (presumably due to the ventral path of the retractor sheath).

Accordingly, results suggest that maldanins have a axially-modified ventral proboscis. The axial modification refers to the tube-like appearance of the everted proboscis. However, because the appearance of the tube is asymmetrical (due to the ventral sac), the retractor sheath is ventrally oriented, and a muscle bulb may be present, I consider the structure more consistent with the ventral proboscis category. TZETLIN (1991) provides a hypothesis of proboscideal evolution within the order Capitellida in which the ventral state is considered more primitive than the axial state. Perhaps the axially-modified ventral proboscis of maldanins represents an intermediate state in TZETLIN's (1991) hypothesis.

Within Maldaninae, several features are variable. Because this study only compares a single representative of each genus, it is not possible to comment on consistency of features within each genus. However, results do permit some comment regarding features considered of generic importance, and does suggest other features that may be promising to investigate.

With regard to the cephalic rim, LIGHT (1991) considered the development and shape of the lateral borders and their separation from the palpode as a generic feature. An additional characteristic that may contribute to descriptions of this feature is the development of the notch or cleft that may separate the borders and palpode.

LIGHT (1991) recognized three shapes of Maldaninae palpode; spade-like, mushroom-shaped, and indistinct. Results indicate that shape categories are variable within some genera. For example, LIGHT characterized the palpode of *Asychis* as spade-like, and that of *Metasychis* as mushroom-shaped; however, the examined *Asychis amphiglyptus* has a rounded palpode, and the examined *Metasychis disparidentatus* has a spade-like palpode. It is suggested that descriptions of shape may be improved by considering the profile and thickness of the palpode.

LIGHT (1991) characterized maldanin nuchal organs as four basic shapes (J-shaped, U-shaped, slightly curved, and crescentic). Additional categories are needed to describe nuchal organs in which the stems diverge (as in *Sonatsa*) and in which both stems and tips diverge (as in *Bathyasychis*). It is suggested that descriptions of nuchal organs include reference to stem and tip shape and length. The internuchal muscle appears to relate to characteristics of the nuchal organs (e.g., shape and length), and additional study of this muscle is warranted. The internuchal muscle, which may be prominent in maldanins, has not been investigated for other maldanids.

A cephalic keel, though not considered a generic character by LIGHT (1991), was considered so in the past. Results indicate that the usefulness of the keel as a taxonomic character may be improved by taking into consideration compressibility and width when evaluating the more traditional height and length characters. Examinations of muscle development provides a means to cross check keel designations.

Source : MNHN, Paris

Features of the proboscis vary among the examined species. *Bathyasychis* and *Sonatsa* are similar in having the densest concentrations of transverse muscles beneath the ventral sac, and the largest volume proboscides of the examined species. It is not known whether these similarities are due to feeding in a similar environment (both co-occur at abyssal depths in trenches) or close phylogenetic relationship. Because both taxa have nuchal organs with diverging stems (the tips also diverge in *Bathyasychis*), another feature suggests relationship.

In the past it was questioned whether *Sonatsa* was distinct from *Maldane* since they are morphologically similar (ARWIDSSON, 1922; DETINOVA, 1985b). GREEN (1987) argued for recognition of *Sonatsa* based on nuchal organ shape and the presence of an enlarged ventral glandular pad on setiger 5. The similarities in proboscis development and nuchal organs between *Bathyasychis* and *Sonatsa* support *Sonatsa*'s generic status. So do the differences between *Sonatsa meridionalis* and *Maldane sarsi* in the muscle development of the proboscis, keel, and palpode.

Other species provide an additional example where similarity in external morphology does not correspond with proboscis musculature. For example, *Chirimia lobata* and *Metasychis disparidentatus* have serrate cephalic borders; however, the development of the muscles beneath the ventral sac differ. Proboscis muscles are more similar between *Chirimia lobata* and *Asychis amphiglyptus*; these species also are similar in having well-developed internuchal muscles. Conversely, the appearance of the plaque differs among *Metasychis disparidentatus*, *Maldane sarsi*, and *Sabaco elongatus*, but they are similar in having reduced ventral sac muscles. The internuchal muscle is similar between *Metasychis disparidentatus* and *Maldane sarsi*, but is unique in *Sabaco elongatus*.

Although it is not known at this time which features are more reflective of convergence or relationship, this study supports the status of the genera. It also supports the view that important features include the development of the cephalic rim and nuchal organs. I suggest that proboscis musculature, keel development, and palpode shape may be important, but need further study.

## ACKNOWLEDGEMENTS

Special thanks go to Leslie HARRIS of the Allan Hancock Foundation for the loan of specimens. Larry LOVELL generously allowed use of his microscope with drawing tube. Discussions with Dr. Kirk FITZHUGH prompted me to prepare this paper, and I appreciate his interest. I am grateful to Drs. Jerry KUDENOV, Alexander TZETLIN, and two anonymous reviewers for their comments to an earlier draft of this paper.

## REFERENCES

ARWIDSSON, I., 1907. — Studien über die skandinavischen und arktischen Maldaniden nebst Zusammenstellung der übrigen bisher bekannten Arten dieser Familie. *Zool. Jhrb., Suppl.*, **9** : 1-308.

ARWIDSSON, I., 1922. — Systematic notes on some maldanids. *Svenska Vetensk. Akad. Stockholm, Hand.*, **663** :1-46.

DALES, R.P., 1962. — The polychaete stomodeum and the inter-relationships of the families of Polychaeta. *Proc. Zool. Soc. Lond.*, **139** : 389-428.

DETINOVA, N.N., 1985a. — Taxonomy, composition and distribution of polychaetes of the subfamily Lumbriclymeninae (Maldanidae). *In: Polychaeta: Morphology, systematics, ecology. Proc. USSR Polychaeta Conference, Leningrad, 1983* : 25-29. [in Russian].

DETINOVA, N.N., 1985b. — The taxonomic significance of the structure of the parapodia in some Maldanidae (Polychaeta). *Zool. Zh.*, **64** : 1487-1492. [in Russian].

FAUCHALD, K., 1972. — Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. *Allan Hancock Monogr. mar. Biol.*, **7** : 1-575.

FAUCHALD, K., 1977. — The polychaete worms: Definitions and key to the orders, families and genera. *Nat. Hist. Mus. Los Angeles County, Sci. Ser.*, **28** :1-190.

GREEN, K.D., 1987. — Revision of the genus *Sonatsa* (Polychaeta: Maldanidae). *Bull. Biol. Soc. Wash.*, **7** : 89-96.

IMAJIMA, M. & Y. SHIRAKI, 1982. — Maldanidae (Annelida: Polychaeta) from Japan (Part 1,2). *Bull. Nat. Sci. Mus., Tokyo*, **8** : 7-88.

Source : MNHN, Paris

LIGHT, W.J.H., 1991. — Systematic revision of the genera of the polychaete subfamily Maldaninae Arwidsson. *Ophelia Suppl.*, **5** : 133-146.

ORRHAGE, L., 1973. — Two fundamental requirements for phylogenetic-scientific works as a background for an analysis of Dale's (1962) and Webb's (1969) theories. *Z. Zool. Syst. Evolut.-forsch.*, **11** : 161-173.

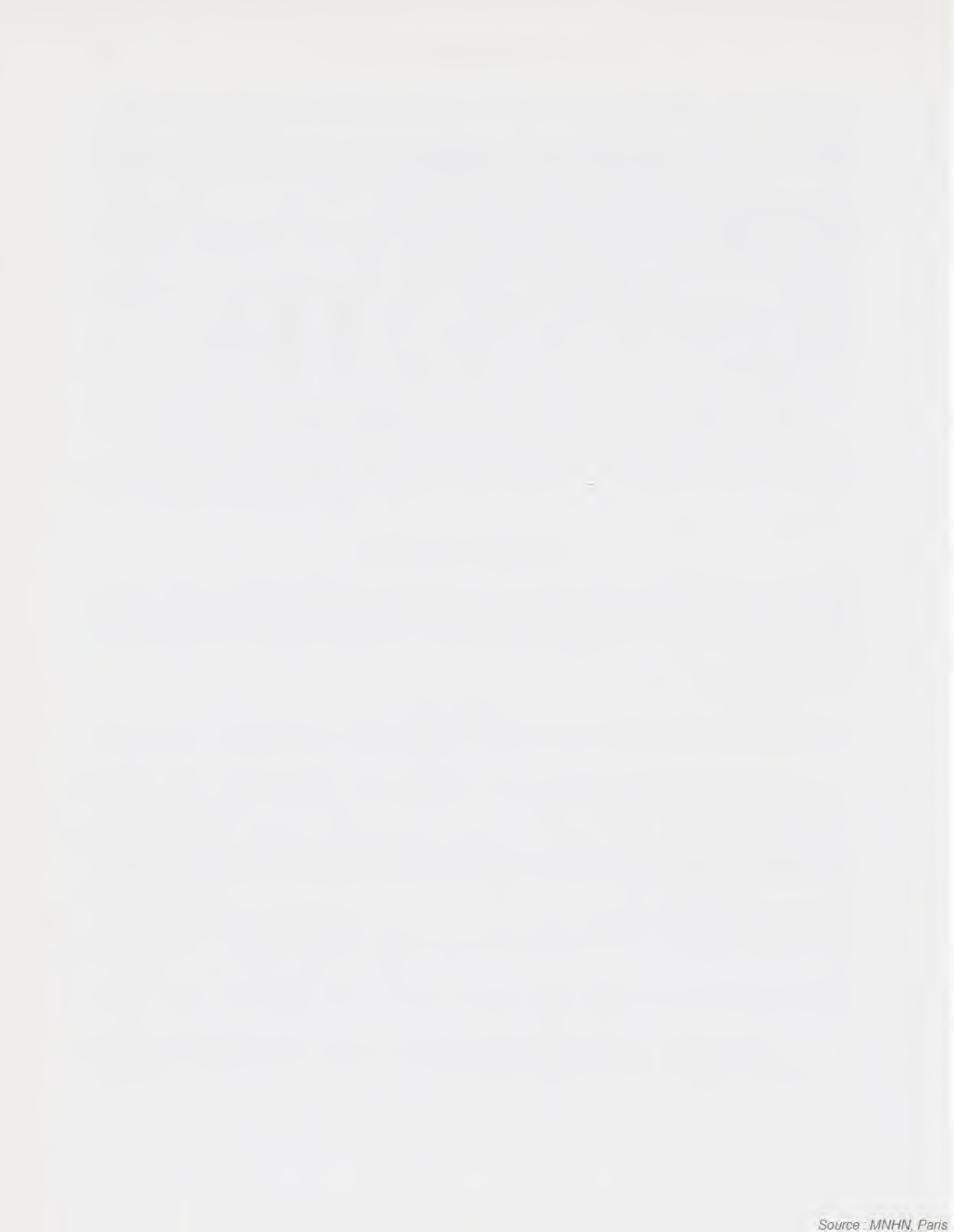
PILGRIM, M., 1966. — The morphology of the head, thorax, proboscis apparatus and pygidium of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi*. *J. Zool., Lond.*, **148** :453-475.

PURSCHKE, G., 1988. — XI. Pharynx. *In* W. WESTHEIDE & C. O. HERMANS (eds), The Ultrastructure of Polychaeta. *Microfauna Marina*, **4** : 177-197. Gustav Fischer Verlag, Stuttgart, New York.

TZETLIN, A.B. 1991. — Evolution of feeding apparatus in the polychaetes of the order Capitellida. *Zool. Zh.*, **70** : 10-22. [in Russian].

ULLMAN, A. & C.G. BOOKHOUT, 1949. — The histology of the digestive tract of *Clymenella torquata* (Leidy). *J. Morph.*, **84** : 31-55.

Source : MNHN, Paris



Source : MNHN, Paris

# Effects of sample fixation on body shape of *Capitella capitata* (Polychaeta, Capitellidae)

*María Nuria MÉNDEZ & María José CARDELL*

Departament d'Ecologia, Facultat de Biologia
University of Barcelona
Avda. Diagonal 645
08028 Barcelona Spain

SUMMARY

Formaldehyde fixed specimens of *Capitella capitata* from the littoral zone of Barcelona showed several body forms : "contracted *C. capitata*" (CC) - pointed prostomium, contracted thorax, anterior setigers distinct; "elongated *C. capitata*" (EC) - triangular prostomium/peristomium, elongated thorax, anterior setigers indistinct; "intermediate *C. capitata*" (IC) - intermediate form between CC and EC. Five fixation tests were performed using different formaldehyde concentrations, sieving or unsieving before fixation, and different periods between sample collection and fixation. By these tests it was shown that CC is the regular form, whereas EC and IC are caused by deficiencies in sample fixation. Recommendations are given for avoiding the fixation aberrant fixation forms which might impair studies in taxonomy and population dynamics of this species.

RÉSUMÉ

**Effets de la fixation des échantillons sur la forme du corps de *Capitella capitata* (Polychaeta, Capitellidae)**

Des spécimens préservés de *Capitella capitata* du littoral de Barcelone montrent plusieurs formes du corps : "*C. capitata* contractée" (CC) - prostomium pointu, thorax contracté, sétigères antérieurs bien differenciés ; "*C. capitata* allongée (EC) - prostomium/peristomium triangulaire, thorax allongé, sétigères antérieurs pas différenciés ; "*C. capitata* intermédiaire" (IC) - forme intermédiaire entre CC et EC. Cinq expériences de fixation ont été effectuées avec différentes concentrations de formol, tamisage et pas de tamisage des échantillons avant la fixation et différentes périodes de temps entre le prélèvement et la fixation. Les résultats indiquent que CC est la forme régulière, tandis que EC et IC sont le résultat des imperfections de la fixation des échantillons. On propose plusieurs recommandations pour éviter les formes aberrantes comme conséquence du procédé de fixation qui peut contrarier les études de systématique et de dynamique des populations de cette espèce.

## INTRODUCTION

Traditional procedures for treating soft-bottom samples to obtain benthic macrofauna were given, among

MÉNDEZ, M.N. & M.J. CARDELL, 1994. — Effects of sample fixation on body shape of *Capitella capitata* (Polychaeta, Capitellidae). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 111-117. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

others, by BANSE & HOBSON (1974), FAUCHALD (1977), and ELEFTHERIOU & HOLME (1984). Those techniques include screening and fixation of samples which may cause alterations to the organisms such as contraction or damage to soft-bodied animals. Degrees of contraction may vary in some organisms and therefore, changes are unpredictable and possibly resulting confusions in identifications.

In previous studies of benthic macrofauna from the littoral zone of Barcelona several body forms of preserved specimens of *Capitella capitata* (FABRICIUS, 1780) were observed (ROS *et al.*, 1990; ROS & CARDELL, 1991; FLOS & SERRA, 1992). The different body shapes are found in the same preserved sample and which have not been distinguished in live specimens. This suggests that treatment of samples may modify the body form of this species thus impairing taxonomy and population dynamics research. In view of future studies it is of interest to determine which sample treatments may produce changes in the body shape of *C. capitata*.

## MATERIAL AND METHODS

Bottom samples were collected by SCUBA diving from the upper 10 cm of sediment near the Olympic Harbour of Barcelona (15 m depth) between February and May 1992. The sediment in this site was fine sand (0.125 - 0.250 mm).

Five different tests were designed to evaluate single and combined effects of the following variables of fixation: formaldehyde concentration, screening of samples and time between collection and fixation of samples.

Test 1. — Formaldehyde concentration.

Live specimens were sorted from the sediment and submerged in 11 different solutions of formaldehyde in sea water (from 0.1 to 4%).

Test 2. — Formaldehyde concentration and screening of samples.

Twenty samples of sediment were collected. The combined effect of the following two variables was tested: sieving (through a 0.5 mm mesh) or unsieving samples before fixation and formaldehyde concentration (1 and 4%). Five replicates from each combination were obtained.

Test 3. — Time.

Sixteen samples of sediment were collected. The combined effect of the following three variables was tested: sieving (0.5 mm) or unsieving samples before fixation, formaldehyde concentration (1 and 10%) and time between collection and fixation (0, 2, 4 and 6 hours).

In both test 2 and test 3, sieved samples consisted of 125 ml of sediment and 62.5 ml of seawater, while unsieved samples consisted of 250 ml of sediment and 125 ml of seawater. The different formaldehyde concentrations were calculated according to the volume of the overlying water by the addition of concentrated formaldehyde.

Test 4. — Presence of sediment.

Each of 100 live specimens was transferred to separate jars with 2 ml of a 4% formaldehyde solution, and each of 100 live specimens was covered by a 3 mm layer of fine sand and fixed by the addition of 2 ml of a 4% formaldehyde solution.

Test 5. — Volume of sediment.

Five samples of different volumes of sediment were placed and fixed with a 4% formaldehyde solution inside cylindrical sample jars of several sizes wich were turned several times. After 24 hours of sedimentation, each sample was divided in three horizontal layers and each level was analyzed separately.

Individuals of the different body shapes were counted in all the tests. A two way ANOVA test and Pearson's correlations were performed to assess the effect of these variables on the body shape of *C. capitata*.

## RESULTS

Three different body forms of *C. capitata* were distinguished according to their thorax shape. They were called "contracted *C. capitata*" (CC),"enlarged *C. capitata*" (EC) and "intermediate *C. capitata*" (IC). CC has a rather pointed prostomium partially withdrawn back into the contracted first setiger, indistinct peristomium and thoracic setigers are strongly distinct (wider than they are long). EC presents a prostomium and peristomium with a broadly rounded triangular shape, thoracic setigers indistinct (slightly broader than they are long) and a slender thorax. IC presents an intermediate thorax shape between CC and EC and has a rather pointed prostomium partially withdrawn

Source : MNHN, Paris

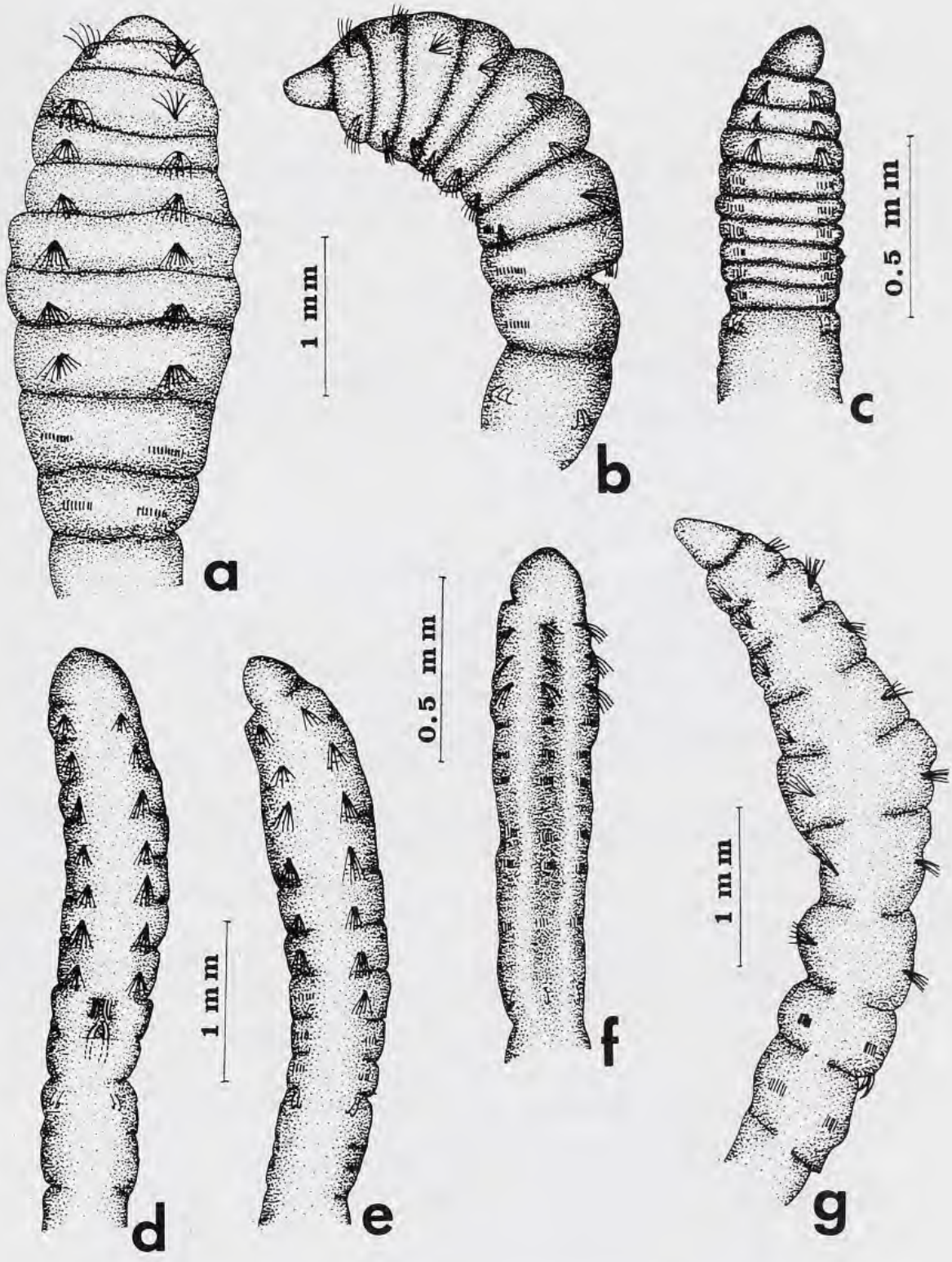



FIG. 1. — Anterior end of "contracted *Capitella capitata*" (CC): **a**, dorsal view (female). **b**, lateral view (male). **c**, lateral view (juvenile). Anterior end of "elongated *C. capitata*" (EC): **d**, dorsal view (male). **e**, lateral view (female). **f**, lateral view (juvenile). Anterior end of "intermediate *C. capitata*" (IC): **g**, lateral view (male).

Source : MNHN, Paris

back into the contracted first setiger, indistinct peristomium, and thoracic setigers slightly distinct (slightly broader than they are long) (Fig. 1).

Since CC was dominant form in the samples, results only show frequency of EC and IC which were considered as the modified forms.

Test 1. — Formaldehyde concentration.

Relative abundances of IC increased with low concentrations of formaldehyde (<0.2%) (Table 1). EC did not occur. Therefore, individuals which are fixed with low concentrations of formaldehyde probably die slowly and relaxed thus producing the characteristic enlargement of thorax from IC. This agrees with the suggestion given by BANSE & HOBSON (1974) about a relaxed state of animals obtained with few drops of concentrated formaldehyde in 1 litre of sea water.

TABLE 1. — Frequency of "elongated *Capitella capitata*" (EC) and "intermediate *C. capitata*" (IC) at various formaldehyde concentrations (F.C.). N = total number of *C. capitata*.

| | | Frequency (%) | |
|---|---|---|---|
| F.C. (%) | N | EC | IC |
| 0.1 | 27 | 0 | 48 |
| 0.2 | 24 | 0 | 17 |
| 0.3 | 28 | 0 | 0 |
| 0.4 | 14 | 0 | 0 |
| 0.5 | 34 | 0 | 8.8 |
| 0.6 | 16 | 0 | 0 |
| 0.7 | 20 | 0 | 0 |
| 0.8 | 22 | 0 | 0 |
| 0.9 | 12 | 0 | 0 |
| 1.0 | 281 | 0 | 1 |
| 4.0 | 130 | 0 | 0 |

Test 2. — Formaldehyde concentrations and screening of samples.

EC was only present in unsieved samples. Its relative abundance was slightly higher at 1% than at 4% formaldehyde (Table 2).

The two way ANOVA test showed a significant difference in the relative abundance of EC on sieved/unsieved samples ($F= 10.206$, $p= 0.006$). No significative differences were obtained related to formaldehyde concentrations ($F= 1.506$, $p= 0.238$).

The unsieving procedure seems to be the most important factor to obtain higher quantities of EC. Nevertheless, a slight formaldehyde concentration effect was observed.

TABLE 2. — Frequency of "elongated *Capitella capitata*" (EC) in sieved and unsieved samples fixed with 1 % and 4 % formaldehyde. Total number of *C. capitata* between brackets.

| | Frequency of EC (%) at formaldehyde concentration | |
|---|---|---|
| | 1 (%) | 4 (%) |
| | 0 (423) | 0 (705) |
| SIEVED | 0 (280) | 0 (584) |
| | 0 (401) | 0 (455) |
| SAMPLES | 0 (382) | 0 (488) |
| | 0 (295) | 0 (527) |
| | 13.7 (270) | 3.9 (282) |
| UNSIEVED | 6.4 (328) | 6.3 (269) |
| | 0.5 (381) | 2.2 (273) |
| SAMPLES | 9.8 (265) | 1.4 (286) |
| | 0.5 (210) | 0.7 (286) |

Source : MNHN, Paris

Test 3. — Time.

When fixation was performed directly after sampling, EC was only present in unsieved samples (as in test 2). Nevertheless, when fixation was performed later, EC appeared in sieved and unsieved samples. The relative abundance was not always higher in unsieved samples. No significative correlations were observed between time and the other tested variables (Table 3).

TABLE. 3. — Frequency of "elongated *Capitella capitata*" (EC) in sieved and unsieved samples fixed with 1% and 4% formaldehyde at different times after their collection. Pearson's correlations (r) are calculated between time and frequency of EC obtained for each procedure. Total number of *C. capitata* betwenbrackets. F.C. = formaldehyde concentration.

| | | Frequency of EC (%) for fixation after : | | | | Pearson's correlations |
|---|---|---|---|---|---|---|
| | F.C. (%) | 0 h | 2 h | 4 h | 6 h | (n= 4) |
| SIEVED SAMPLES | | 0 (443) | 0.4 (789) | 38 (490) | 0 (552) | r= 0.256 |
| | | 0 (680) | 2 (438) | 0.1 (628) | 0.7 (404) | r= 0.028 |
| UNSIEVED SAMPLES | | 72 (254) | 0.8 (118) | 7.5 (132) | 25 (394) | r= -0.540 |
| | | 0 (344) | 52 (406) | 10 (312) | 0.4 (502) | r= -0.213 |

Depletion of oxygen in sediments has been reported to cause the organisms to crawl near the sediment surface (BANSE & HOBSON, 1974). Results obtained in tests 1 and 2 suggest that lower quantities of EC could result in samples fixed several hours after their collection than in samples fixed directly after sampling. Hence, a higher percentage of individuals wich have a CC shape could be expected when samples are fixed after several hours due to the upward migration of individuals and the impact of a formaldehyde concentration near to 40 %. However, our results did not confirm this hypothesis. It is suggested that time produces an unpredictable effect on the amount of EC.

Test 4. — Presence of sediment.

Fourteen percent of isolated specimens fixed under sediment belonged to EC, whereas this form was not present among individuals fixed without sediment. A thin layer of sediment, appears sufficient to change the body shape of some individuals. This was confirmed in test 5.

Test 5. — Volume of sediment.

Results given in Table 4 show that there was a direct relationship between percentage of EC and volume of sediment inside a jar. Also a gradient was observed: the lower layers had the highest percentages of EC. Correlations between cumulative volumes (from upper to lower layers) and relative abundance of EC were highly significative ($r= 0.939$, $p< 0.01$, $n= 13$). High frequencies of EC may be caused by compression increasing and formaldehyde diffusion decreasing with sample volume.

TABLE 4. — Frequency of "elongated *Capitella capitata*" (EC) in five samples of different volumes of sediment divided in three equal layers inside a jar. Total number of *C. capitata* between brackets.

| | Frequency of EC (%) in different volumes of sediment | | | | |
|---|---|---|---|---|---|
| LAYER | 100 ml | 200 ml | 500 ml | 1000 ml | 1800 ml |
| UPPER | 0 (3) | 0 (27) | 2.6 (190) | 12.0 (241) | 3.7 (106) |
| MEDIUM | 0 (6) | 0 (41) | 12.6 (214) | 19.1 (507) | 38.3 (201) |
| LOWER | 0 (6) | 0 (173) | 23.8 (231) | 20.4 (401) | 59.3 (221) |

Results obtained in the five tests suggest that the simultaneous presence of the CC, EC and IC in a sample can be explained by the combined effect of formaldehyde concentration and sediment. Lower formaldehyde concentrations, during fixation, may induce organisms to change from a contracted (CC) to a more relaxed shape

Source : MNHN, Paris

(EC). The combined effect of sediment and formaldehyde in an unsieved sample inside a jar may be explained due to the thickness of the sediment which can delay the diffusion of formaldehyde, and prolonging death. The presence of large amounts of sediments may be responsible of an increase in the quantities of EC.

## DISCUSSION

Traditional techniques used in taxonomy of polychaetes are based on collection, screening (before fixation), fixation and preservation. Nevertheless, in population dynamics studies of *C. capitata*, fixation is generally performed before screening (WARREN, 1976; TSUTSUMI & KIKUCHI, 1984; TSUTSUMI, 1987). When fixation is performed before screening, some EC and IC may be present and thus result in errors of taxonomy and populations dynamics:

- Taxonomy. The evident peristomium of EC can be confused with the achaetous first segment of the genus *Capitomastus*, although there are some other features to distinguish between both genera. This confusion has recently been studied by WARREN (1991).
- Population dynamics. Population dynamics studies of *C. capitata* are performed by different thoracic measures (WARREN, 1976; TSUTSUMI & KIKUCHI, 1984; TSUTSUMI, 1987; MARTIN, 1991), which may be strongly affected by treatment of samples, so erroneous interpretations can be obtained.

## CONCLUSIONS

Treatment of soft-bottom samples during fixation may affect the shape of fixed *C. capitata*. Body shapes were related to different combinations of the tested variables. The elongated thorax of IC seems to be associated with low formaldehyde concentrations. Fixation of samples without sieving may produce an increase in the frequency of EC: compression and weight of sediment inside a sample jar affect the shape of *C. capitata*, probably because of decreased formaldehyde diffusion and mechanically prevented body contraction.

Mistakes in taxonomy and population dynamics studies can result from inappropiate fixing procedures. Therefore, to avoid fixation anomalies in *C. capitata* it is recommended:

- Sieve the sample before fixation to avoid effects by compressed sediments. If this is not possible, fix small volumes of sediment (e.g. 200 ml) in several sample jars to allow the diffusion of formaldehyde and to minimize compression.
- Ensure that fixation is done at least at 4% formaldehyde, particularly if the sample cannot be sieved before fixation.
- Turn the sample jar several times after fixation for about 15 minutes to be certain that all the individuals have died.
- Maintain the time between collection and fixation constant during the study.

## ACKNOWLEDGMENTS

This research was supported by the Villa Olímpica, S.A., Barcelona. We are grateful to Dr. Rafael SARDÁ Dr. Josep M. GILI and Dr. Jordi FLOS for their advice and comments on the manuscript. We wish to thank Dr. Judith GRASSLE for her constructive comments.

## REFERENCES

BANSE, K. & K. D. HOBSON, 1974. — Benthic errantiate polychaetes of British Columbia and Washington. *Bull. Fish. Res. Board Can.*, **185** : 1-111.

ELEFTHERIOU, A. & H. HOLME, 1984. — Macrofauna techniques. *In:* N.A. HOLME & A. D. MCINTYRE (eds), *Methods for the study of marine benthos*. Blackwell Scientific Publications. Oxford : 140-216.

FAUCHALD, K., 1977. — The polychaete worms. Definitions and keys to the orders, families and genera. *Nat. Hist. Mus. Los Ang. County Sci. Ser.*, **2** : 1-188.

Source : MNHN, Paris

FLOS, J. & J. SERRA, 1992. — *Repercusió ecològica i geodinàmica de les actuacions en el front marítim de llevant de Barcelona*. Informe tècnic, V.O.S.A., Barcelona, 144 pp.

MARTIN, D., 1991. — *Macroinfauna de una bahía mediterránea: estudio de los niveles de organización de las poblaciones de anélidos poliquetos*. Doctoral Thesis. U. Barcelona, 456 pp.

ROS, J.D., CARDELL, M.J., ALVA, V., PALACIN, C. & I. LLOBET, 1990. — Comunidades sobre fondos blandos afectados por un aporte masivo de lodos y aguas residuales (litoral frente a Barcelona, Mediterráneo occidental) : resultados preliminares. *Bentos* **6** : 407-423.

ROS, J.D. & M.J. CARDELL, 1991. — Effect on benthic communities of a major input of organic matter and other pollutants (coast off Barcelona, Western Mediterranean). *Toxicol. Environ. Chem.*, **31-32** : 441-450.

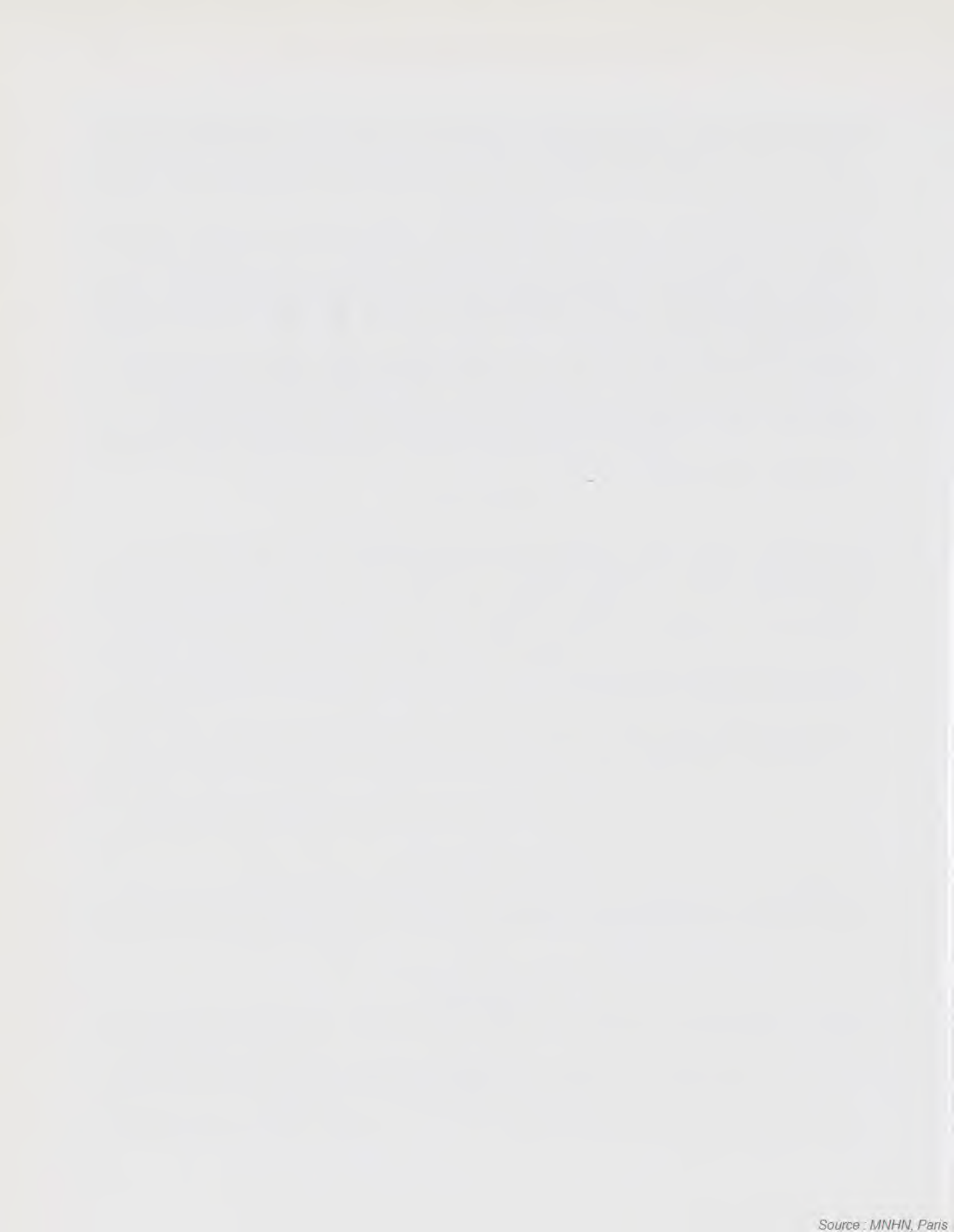
TSUTSUMI, H., 1987. — Population dynamics of *Capitella capitata* (Polychaeta: Capitellidae) in an organically polluted cove. *Mar. Ecol. Prog. Ser.*, **36** : 139-149.

TSUTSUMI, H. & T. KIKUCHI, 1984. — Study of the life history of *Capitella capitata* (Polychaeta: Capitellidae) in Amakusa, South Japan including a comparison with other geographical regions. *Mar. Biol.*, **80** : 315-321.

WARREN, L.M., 1976. — A population study of the polychaete *Capitella capitata* in Plymouth. *Mar. Biol.*, **38** : 209-216.

WARREN, L.M., 1991. — Problems in Capitellid taxonomy. The genera *Capitella*, *Capitomastus* and *Capitellides* (Polychaeta). *Ophelia*, suppl. **5** : 275-282.

Source : MNHN, Paris



Source : MNHN, Paris

# Ultrastructure of sense organs and the central nervous system in *Parenterodrilus taenioides* and their phylogenetic significance in the taxon Protodrilida (Annelida, Polychaeta)

*Günter PURSCHKE * & Claude JOUIN-TOULMOND ***

* Spezielle Zoologie, Fachbereich 5
Universität Osnabrück
D-49069 Osnabrück, Germany
** Biologie et Physiologie des Organismes Marins
Université Pierre et Marie Curie
4, place Jussieu
F-75252 Paris Cedex 05, France

SUMMARY

The following sense organs palps, nuchal organs, and presumed unpigmented ocelli, as well as the central nervous system were investigated by electron microscopy in *Parenterodrilus taenioides*. The palps are mobile sensory structures bearing motile cilia and four types of sensory cells, including presumed phaosomous ocelli. The palp canals are small, filled with cell bodies of muscle cells and a few coelenchyme cells. The canals are covered by a cord of coelenchyme cells. The comparatively large nuchal organs are identical in structure with those of the other Protodrilida. There are two types of presumed ocelli located in posterior ganglionic expansions of the brain. The palps are innervated by three nerves originating from the dorsal and ventral roots of the circumoesophageal connective. The most exceptional features of the brain are four ganglionic expansions extending far posteriorly into the head segment. The lateral ones fuse with the small dorsal root of the circumoesophageal connectives. These findings are compared with the sense organs and the nervous system of the other Protodrilida. They clearly corroborate the supposed relationship of the Protodrilida and additional autapomorphies demonstrate the derived position of *P. taenioides*.

RÉSUMÉ

**Ultrastructure des organes sensoriels et du système nerveux central de *Parenterodrilus taenioides* et leur signification phylogénétique chez les Protodrilida (Annélides Polychètes)**

Les organes sensoriels tels que palpes, organes nucaux, structures assimilées à des ocelles non pigmentés, ainsi que le système nerveux central ont été étudiés au niveau ultrastructural chez *Parenterodrilus taenioides*. Les palpes sont des appen-

PURSCHKE, G. & C. JOUIN-TOULMOND, 1994. — Ultrastructure of sense organs and the central nervous system in *Parenterodrilus taenioides* and their phylogenetic significance in the taxon Protodrilida (Annelida, Polychaeta). *In:* J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 119-128. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

dices sensoriels ciliés et mobiles qui portent quatre types de cellules sensorielles, dont des ocelles de type phaosome. Les canaux internes des palpes sont minces, remplis par les corps cellulaires des cellules musculaires et par quelques cellules du coelenchyme qui forment aussi un cordon cellulaire à la périphérie de chaque canal. Les palpes reçoivent trois nerfs issus des racines dorsales et ventrales des connectifs périoesophagiens. Les organes nucaux, relativement larges, ont une structure identique à ceux des autres Protodrilida. Deux autres types de structures, assimilées à des ocelles non pigmentés, sont logées dans des expansions ganglionnaires postérieures du cerveau. Les caractéristiques les plus remarquables du cerveau sont ces quatres expansions ganglionnaires qui s'étendent loin vers l'arrière, dans le segment céphalique. Les expansions les plus latérales fusionnent avec les petites racines dorsales des connectifs périoesophagiens. Ces caractères sont comparés à ceux des autres Protodrilidés et les nouvelles autapomorphies révélées par ce travail démontrent que *P. taenioides* est une forme dérivée. L'ensemble des résultats confirme les relations prélablement établies au sein des Protodrilida.

## INTRODUCTION

The Protodrilida are interstitial polychaetes characterized by a long and slender body, reduced or absent parapodia, a pair of prostomial appendages (palps), and a pygidium generally with two adhesive lobes. The about 60 known species of the taxon belong to only four genera: *Saccocirrus* Bobretzky, 1871, *Protodrilus* Hatschek, 1880, *Protodriloides* Jouin, 1966 and *Parenterodrilus* Jouin, 1992. Electron microscopic investigations were conducted to clarify the functional morphology of selected organs as well as to test the proposed monophyly of the Protodrilida and their subordinate taxa, to evaluate their relationship and to find synapomorphies with their supposed sister group, the Spionida (e.g., PURSCHKE & JOUIN, 1988; PURSCHKE, 1990a, 1993). In contrast to the small body size and the apparently simple organization of these polychaetes, their sense organs and the central nervous system turned out to be rather complex structures when investigated by electron microscopy (EAKIN *et al.*, 1977; PURSCHKE, 1990a, 1990b, 1990c, 1992, 1993; PURSCHKE & JOUIN-TOULMOND, 1993). Therefore, these structures provide numerous characters which might be useful for phylogenetic considerations.

Sense organs present in every species are: the palps, the nuchal organs, and various types of unpigmented presumed ocelli. Pigmented ocelli only occur in the *Saccocirrus* species and a few *Protodrilus* species. These structures have now been investigated in species of every genus except the monotypic *Parenterodrilus*, which is so far only known from sublittoral coral sands of the island of Moorea, French Polynesia. *Parenterodrilus taenioides* is especially remarkable because it is the only known polychaete possessing a vestigial alimentary canal, without mouth and digestive cavity (JOUIN, 1979, 1992). Thus, the main purpose of the present investigation was to clarify the functional morphology of the sense organs and the central nervous system of this rare species, in order to use these supplementary data for a comprehensive phylogenetic discussion of the Protodrilida. The present findings fit very well into a dendrogram showing the presumed relationship of the subordinate taxa of the protodrilidans which has previously been suggested (PURSCHKE & JOUIN, 1988) and which can now be based on an even larger number of characters.

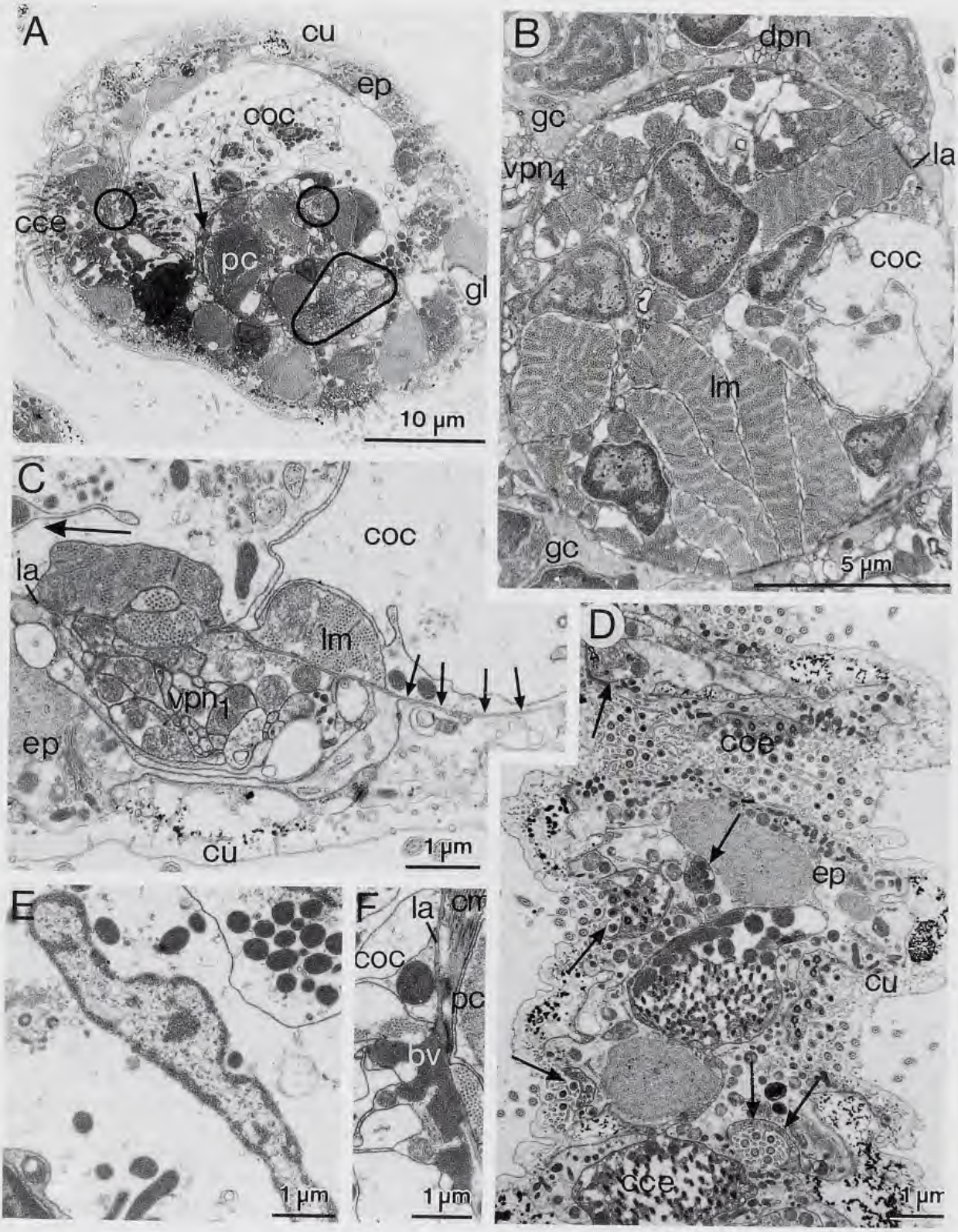
## MATERIAL AND METHODS

Specimens of *P. taenioides* were collected by the junior author in sublittoral sands of the barrier reef at the type locality in Moorea, French Polynesia (JOUIN, 1979). After relaxation in a mixture of equal parts of sea water and 7.7 % $MgCl_2$, specimens were fixed in a cacodylate buffered (0.2 M, pH 7.4) solution of 2 % glutaraldehyde, adjusted with NaCl to about 1,300 mosM for 1 h. They were rinsed in the same buffer, postfixed in buffered 1% $OsO_4$, dehydrated in an ethanol series, and embedded in Epon. Ultrathin sections of two specimens were cut with a diamond knife on a Reichert Ultracut E microtome and ribbons of sections were collected on single slot grids coated with pioloform support film in order to obtain complete series of ultrathin sections. They were stained in an

---

FIG. 1A-F. — *Parenterodrilus taenioides*. Palps. A. Low power TEM micrograph of cross section appr. 25 µm above the palp base; center occupied by palp canal (*pc*) and coelenchyme cells (*coc*); palp nerves encircled; arrow points to position of blood vessel. B. Cross section of palp canal. C. Ventral palp nerve *vpn1* and longitudinal muscle fibres; note disappearance of extracellular lamina (*la*) between coelenchyme and epidermal cells lateral to *vpn1* (*small arrows*); the *large arrow* points to position of palp canal. D. Tangential section of ventral side with ciliated cells (*cce*), epidermal supporting cells (*ep*) and sensory cells (*arrows*). E. Coelenchyme cell with nucleus. F. Blood vessel (*bv*). - *cce* ciliated cell, *cm* circular muscle fibre, *coc* coelenchyme cell, *cu* cuticle, *dpn* dorsal palp nerve, *ep* epidermal supporting cell, *gc* glial cell, *gl* gland cell, *la* extracellular lamina, *lm* longitudinal muscle cell, *pc* palp canal, *vpn1, 4* ventral palp nerve 1,4.

Source : MNHN, Paris




Source : MNHN, Paris

LKB Ultrostainer and examined with a Zeiss EM 109 electron microscope. Reconstruction of the nervous system was done from low power electron micrographs taken at intervals of between 0.7 µm and 3.5 µm, depending on the structures observed.

## RESULTS

In *Parenterodrilus taenioides* the palps arise in an anterior-lateral position from the prostomium. The ciliation of the anterior end is very well developed; in addition to numerous sensory cilia, the palps, prostomium and head segment (= peristomium) bear mobile cilia as well. The nuchal organs are heavily ciliated, rounded areas of about 25 µm diameter at the posterior end of the prostomium. Unpigmented ocelli are not visible with light microscopy.

*Palps.* The palps are circular to oval in cross section. They are composed of cuticle, epidermis, sensory cells, intraepithelial nerves, a palp canal, a small blood vessel, and so-called coelenchyme cells (Fig. 1A-F). The epidermis is comprised of supporting cells, with glandular and ciliated cells distributed among them. The latter are restricted to the ventral side where they are arranged in bands. There are three palp nerves: the medial nerve (*vpn*$_4$; see PURSCHKE, 1993 for terminology) is the largest and contains about 330 nerve fibres; the other nerves are considerably smaller and consist of 15 (*dpn*) and 35 (*vpn*$_1$) fibres. Small branches of these longitudinal nerves form a network of nerve cell processes ventrally, and around the palp canals. Each nerve is partly enveloped by glial cells (Fig. 1B). In the nerve fibres clear vesicles with a diameter of 40-60 nm and dense-cored vesicles of 70-95 nm diameter are present (Fig. 1C). Neuroneuronal and neuromuscular synapses were frequently observed within the nerve tracts.

Each palp has a small canal, 10-15 µm in diameter (Fig. 1A-C, E-F). The canals are situated ventrally in the palps and unite behind the neuropile of the brain. They are filled with muscle cells and a few coelenchyme cells, surrounded by an extracellular lamina. There are only a few small muscle fibres outside the palp canals, most of which are situated close to the small ventral palp nerve (*vpn*$_1$: Fig. 1C). Besides these longitudinal fibres there are a few small circular fibres in the palp canals. The canals are covered dorsolaterally by coelenchyme cells, which are electron-lucent with only very few organelles and an irregular outline (Fig. 1A, C, E). Although of presumably mesodermal origin, this coelenchyme tissue is not separated from the epidermis by a basal lamina on all sides; extracellular material was only detectable between the palp canal and the small palp nerve (Fig. 1C). Each palp is supplied by a small blind-ending blood vessel which is situated at the palp canal opposite to the main palp nerve.

Three types of bipolar sensory cells have been found on the palps and the prostomium (Fig. 2A-F). The monociliary type-1 sensory cells are so-called collar receptors (e.g. SCHLAWNY *et al.*, 1991): the cilium passes through the cuticle and is surrounded by 10 modified microvilli (Fig. 2A-B). A cylinder of electron-dense material lies below the microvilli. It is connected to the ciliary rootlet just underneath the basal body. Proximally, thin filaments originate from this cylinder and enter the microvilli. The dendritic processes are about 1 µm in diameter and contain 3-4 long mitochondria (Fig. 2A). The second type of sensory cell is multiciliary, with 3-9 cilia penetrating the cuticle (Fig. 2C-D). These sensory cells are the most frequent; they either occur in isolation or grouped in two adjacent sensory cells forming a ciliary tuft. The cilia are of different lengths and may be up to 15 µm long. They usually arise from a slight depression of the cell apex, which creates a raised rim at the periphery of the sensory cell (Fig. 2D). The cilia are surrounded by short microvilli and anchored by long rootlets (Fig. 2C). Sensory cells of the third type have non-penetrative (intracuticular) cilia and they may be isolated or clustered in groups of up to 9 sensory cells (Fig. 2E-F). Their long dendritic processes extend above the level of the adjacent epidermal cells and bear one or two horizontal cilia (Fig. 2E). The cilia are about 4 µm long and have a 9x2+0 axoneme (Fig. 2E, inset). Usually they divide in branches in which the microtubules are successively lost.

*Nuchal organs.* The nuchal organs consist of numerous ciliated supporting cells, an average of seven bipolar sensory cells, and a retractor muscle (Fig. 3A-D), which runs ventromedially and attaches to the posterior end of the palp canal. Ciliated supporting cells surround the dendritic processes of the sensory cells forming the olfactory chamber (3.5-4 µm in diameter) in the middle of the ciliated area (Figs 3A, 4). They bear an average of 35 cilia (3.2 cilia per µm$^2$), which are anchored by basal bodies and long striated rootlets. The ciliated supporting cells give also rise to numerous microvilli; these form a paving-stone-like cover above the cuticle, which is only penetrated by the cilia of these cells (Fig. 3B-C). This layer also covers the olfactory chamber. The dilated microvillar tips are cubic in shape, only 20 nm apart and interconnected by fibrillar material (Fig. 3C). Numerous clear vesicles, coated vesicles, coated pits and lysosomes indicate a considerable degree of endo- or exocytosis in

Source : MNHN, Paris

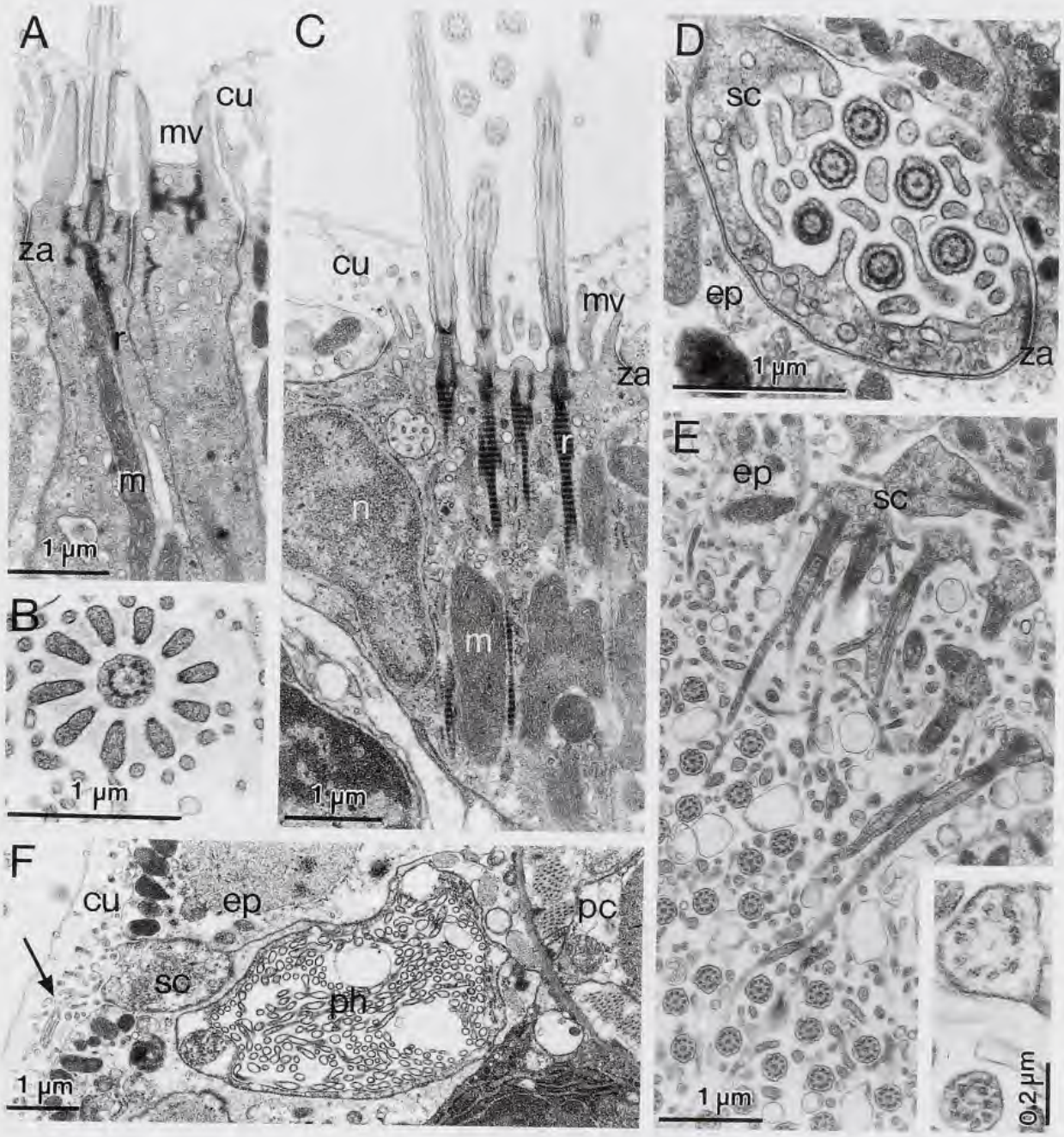



FIG 2A-F. — *Parenterodrilus taenioides*. Sensory cells of palps. A. Collar receptors. B. Cilium and microvilli of collar receptor in cross section. C. Multiciliary sensory cell; nucleus (*n*) situated laterally. D. Cross section of apex of multiciliary sensory cell (*sc*); note clear vesicles accumulating in sensory cell. E. Group of sensory cells with intracuticular cilia; cross sectioned cilia belong to ciliated epidermal cell; inset: sensory cilia in cross section. F. Presumed ocellus with phaosome (*ph*). The *arrow* points to a sensory cell with intracuticular cilium. - *cu* cuticle, *ep* epidermal cell, *m* mitochondrion, *mv* microvillus, *n* nucleus, *pc* palp canal, *ph* phaosome, *r* rootlet, *sc* sensory cell, *za* zonula adhaerens.

Source : MNHN, Paris

these cells (Fig. 3A-B). Each sensory cell bears one cilium with a 9x2+0 axoneme and a few microvilli (Fig. 3A, D). The ciliary rootlets are vestigial: 0.5 µm long and 0.04 µm thick. The ciliary shafts branch. In the branches the microtubules are successively lost, resulting in structures indistinguishable from regular microvilli (Fig. 3D). Microvilli and ciliary branches extend into the subcuticular space above the supportive cells outside the olfactory chamber (Fig. 3A).

*Presumed Ocelli.* In each palp four presumed ocelli (type 1) have been found close to the main palp nerve (Fig. 4). They consist of a single sensory cell characterized by an intracellular vacuole (phaosome) containing numerous microvillus-like ciliary branches (Fig. 2F). There are no pigmented or unpigmented ocelli in the prostomium of *P. taenioides*. However, the type-2 and type-3 unpigmented ocelli are located in the peristomium (= head segment) in the lateral posterior ganglionic expansions of the brain (Figs 3E-F, 4). Each ocellus consists of a sensory cell and a supporting cell forming an extracellular cavity. These cavities are completely filled with microvillus-like branches of two cilia in both types. There are two of the minute type-2 ocelli (3x2x2 µm; Fig. 3E) but five of the type-3 ocelli (18x6x4 µm; Fig. 3F) in each specimen investigated. Other differences concern position, branching pattern of cilia and arrangement of microvilli. The ocelli will be described in more detail separately (PURSCHKE & JOUIN-TOULMOND, 1993).

*Central nervous system.* The neuropile of the brain is situated in the prostomium in the curve formed by the palp canals (Fig. 4). Conspicuous features are two pairs of dorsal expansions (*pe* in Fig. 4) formed by nerve cell processes and, posteriorly, by the perikarya of neurons and glial cells. These expansions extend far into the head segment; the lateral ones contain the presumed ocelli. The ventral nerve cord communicates with the brain through the circumoesophageal connectives (*cc*). Anteriorly, before these nerves turn towards the brain, each connective divides into a ventral (*vrcc*) and a dorsal root (*drcc*). The dorsal roots (*drcc*) and the nerve cell processes of the lateral expansions (*pe*) enter the neuropile together as one nerve. The nuchal nerve (*nn*) very likely emanates from the lateral expansion (*pe*), whereas the medial expansion gives rise to a posteriorly running dorsal nerve (*dn*). Although gut and stomodaeum are residual, the stomatogastric nerves are well-developed and arise ventrally close to the ventral roots of the circumoesophageal connectives (*vrcc*). The main palp nerve ($vpn_4$) emanates laterally from the anterior part of the brain and receives its fibres from a dorsal and a ventral root. The other palp nerves emerge directly from the roots of the circumoesophageal connectives: the second ventral palp nerve ($vpn_1$) from the ventral root and the thin dorsal palp nerve (*dpn*) from the common nerve containing the nerve fibres of the lateral posterior expansion and the dorsal root close to the brain.

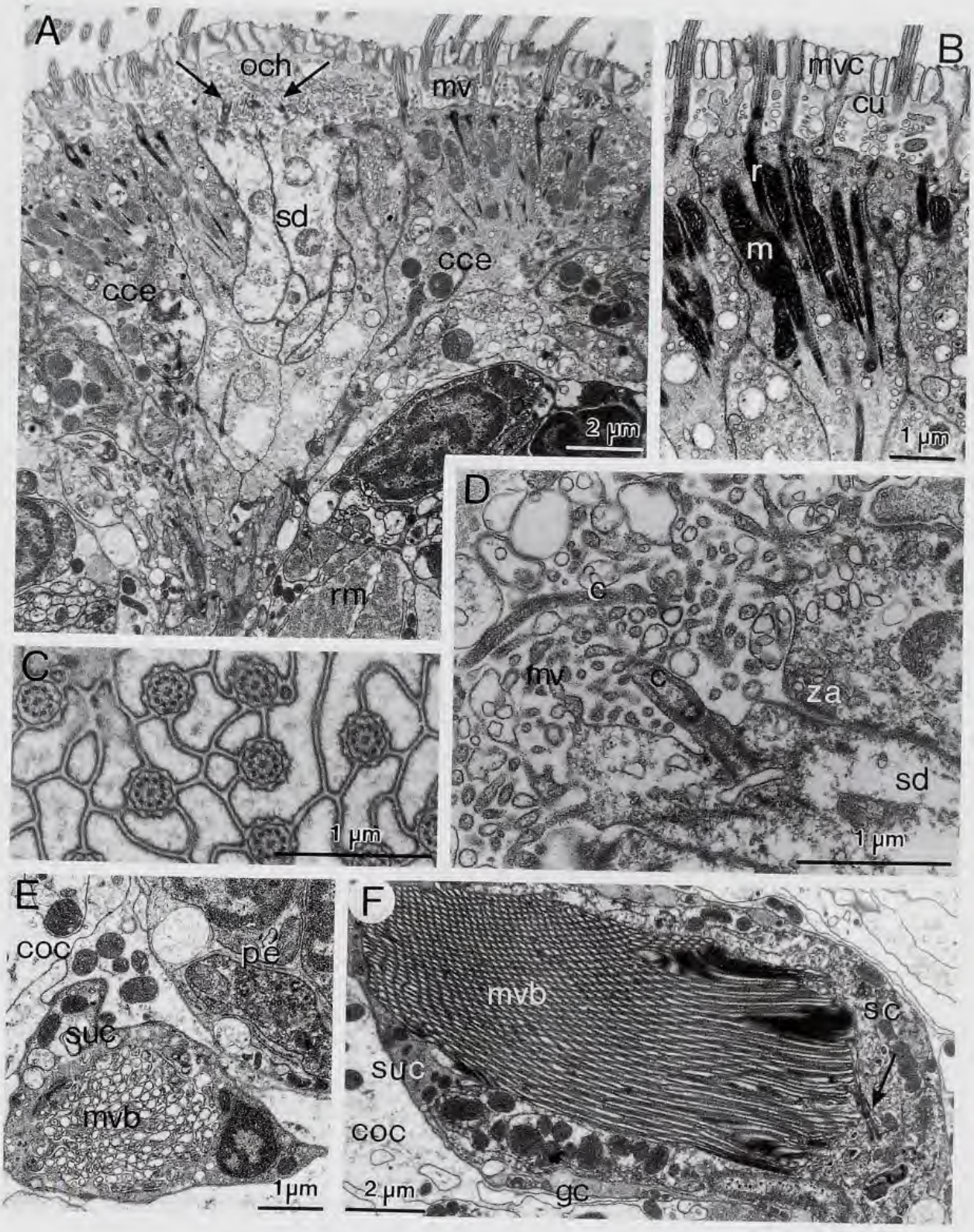
## DISCUSSION

The sense organs and the central nervous system of *P. taenioides* are structurally complex. Although the digestive system is vestigial and not functioning (JOUIN, 1979, 1992), there is no evidence for a reduction of the sensory organs compared with other species of the Protodrilida. However, do these organs provide additional features to elucidate the phylogenetic relationship between them? In a phylogenetic tree previously suggested by PURSCHKE & JOUIN (1988), *Protodrilus* and *Parenterodrilus* were sister groups forming the Protodrilidae which is in turn the adelphotaxon of *Saccocirrus*. Finally, these taxa most likely represent the sister group of *Protodriloides*. Very likely, the taxon Protodrilida is related to the Spionida or one of its subordinate taxa (ORRHAGE, 1974; PURSCHKE & JOUIN, 1988; PURSCHKE, 1993). At present the Protodrilida is still retained, because its sistergroup has not yet been recognized.

The palps of *P. taenioides* are equipped with a variety of sensory cells which allow reception of different sensory stimuli from a wide area around the anterior end. They differ externally from those of *Saccocirrus* and most *Protodrilus* species (except *P. brevis*; see JOUIN, 1970) in the presence of motile cilia (PURSCHKE, 1993). In the Spionida such a ciliation is generally present, located in a groove and used for collecting food particles (DAUER, 1987; FAUCHALD & JUMARS, 1979). Since a mouth is absent in *P. taenioides*, the remaining functions

FIG. 3A-F. — *Parenterodrilus taenioides*. A-D. Nuchal organ. A. Low power micrograph showing entire organ in cross section; *arrows* point to sensory cell cilia; subcuticular space with microvilli (*mv*) and ciliary branches of sensory cells. B. Ciliated cells with cover of microvillar tips (*mvc*). C. Microvillar tips in transverse section. D. Sensory dendrites with cilia (*c*) and microvilli. E-F. Presumed ocelli. E. Small ocellus (type 2). F. Large ocellus (type 3); *arrow* points to sensory cell cilium. - *c* cilium, *cce* ciliated supporting cell, *coc* coelenchyme cell, *cu* cuticle, *gc* glial cell, *m* mitochondrion, *mv* microvillus, *mvb* microvillus-like ciliary branch, *mvc* microvillar cover, *och* olfactory chamber, *pe* posterior expansion of brain, *r* rootlet, *rm* retractor muscle, *sc* sensory cell, *sd* sensory dendrite, *suc* supporting cell, *za* zonula adhaerens.

Source : MNHN, Paris




Source : MNHN, Paris

may be orientation in the interstitial medium and a more rapid exchange of water at the surface of the animal. Since motile cilia are also present on the palps of *Protodriloides*, this character might be a vestige of a more developed ciliation which could be assumed for the last common stem species with the Spionida. The sensory cells with cilia penetrating the cuticle or with non-penetrative cilia are of minor phylogenetic importance, because similar cells have been found in the other Protodrilida and they are not different from sensory cells generally present in annelids (STORCH & SCHLÖTZER-SCHREHARDT, 1988; PURSCHKE, 1993). Among the sensory cells of the palps only the phaosomous ocelli can be considered for phylogenetic considerations. Phaosomes - intracellular cavities containing the presumed light-sensitive organelles - occur only occasionally in polychaetes (PURSCHKE & JOUIN-TOULMOND, 1993,). They are found neither in *Saccocirrus* nor in *Protodriloides* but are present in the palps of several *Protodrilus* species (PURSCHKE, 1993; JOUIN-TOULMOND & MARTIN, unpubl. observ.). These phaosomes are structurally identical with those of *P. taenioides* and, therefore, most likely represent a synapomorphy of *Protodrilus* and *Parenterodrilus*.

With respect to the internal structure, the palps are most similar to those of *Protodrilus*. They differ from those of *Saccocirrus* in the absence of the ampullae, posterior expansions of the palp canals. However, the palp canals are considerably thinner in *P. taenioides*, and the musculature outside the canal and the blood vascular system are reduced compared with *Protodrilus* and *Saccocirrus* (PURSCHKE, 1993). The occurrence of a cord of coelenchyme cells outside the canal and the loss of the external lamina between them and the epidermis are unique for *P. taenioides*. These features are very likely correlated with the absence of podocytes, which form part of the wall of the palp canals in the prostomium of *Protodrilus* and *Saccocirrus* (PURSCHKE, 1993). In these genera the palp canals probably serve as a hydroskeleton filled with movable coelenchyme cells, and the podocytes have been regarded as the site where fluid is introduced into the canals from the blood. Since movable coelenchyme cells, or a fluid-filled lumen, are absent in *P. taenioides*, stiffness of the palps is very likely achieved by the musculature of the palp canals and the external coelenchyme tissue. Consequently, podocytes appear to be redundant.

The nuchal organs of all Protodrilida investigated, including *P. taenioides*, are almost identical in structure and consist of the same types of cells as usually found in polychaetes (PURSCHKE, 1986, 1990a; STORCH & SCHLÖTZER-SCHREHARDT, 1988; RHODE, 1990). In nuchal organs which are not located in deep pits, the ciliated supporting cells generally show structural specialisations which cover and protect the cilia and microvilli of the sensory cells. Paving-stone-like covers of microvillar endings joined by fine fibrils have only been found in the Spionidae *Pygospio elegans* and *Scolelepis squamata* (SCHLÖTZER-SCHREHARDT 1987; RHODE, 1990) and in every species of the Protodrilida, which indicates a high probability of synapomorphy of this character.

The sense organs found in the posterior expansions of the brain in *P. taenioides* show striking similarities to photoreceptors - for example, a great expanse of plasmalemma in the form of microvillus-like cell processes, and the position of the organs beneath the epidermis (EAKIN & HERMANS, 1988). Such presumed ocelli without shading pigment have repeatedly been reported for polychaetes and many species possess at least one type of these ocelli, often in addition to pigmented ones (PURSCHKE, 1992). Their great structural diversity, however, makes it likely that unpigmented ocelli evolved convergently several times in annelids. Unpigmented ocelli are also present in every species of the Protodrilida. Apart from the ocelli (type 1) of the palps, the type-2 and type-3 ocelli of *P. taenioides* are completely different to any ocellus of *Protodrilus*. Due to their different position and structure, the ocelli of *P. taenioides* are not homologous to the so-called statocysts, to the phaosomes or to the pigmented eyes occurring in the prostomium of various *Protodrilus* species (EAKIN *et al.*, 1977; PURSCHKE, 1990b,c). There are also no similarities to the presumed ocelli of *Protodriloides* (unpubl. observ.). On the other hand, there is a certain probability of homology with the type-1 ocelli of *Saccocirrus* (PURSCHKE & JOUIN-TOULMOND, 1993). Since the sister group relationship between *Parenterodrilus* and *Protodrilus* is well established by several synapomorphies, this character may be regarded as a symplesiomorphy taken from the stem species of saccocirrids and protodrilids.

The structure of the central nervous system and the innervation of the anterior end have great potential in phylogenetic reconstruction (ORRHAGE, 1990, 1991). As shown previously, the brain with its nerves and the palp anatomy of *Protodriloides*, *Protodrilus* and *Saccocirrus* give strong evidence for a relationship to the Spionida (PURSCHKE, 1993). As was to be expected, the central nervous system of *P. taenioides* is very similar to that of *Protodrilus* and *Saccocirrus* and corroborates the general pattern observed: e.g., the roots of the circumoesophageal connectives, the stomatogastric nerves and the palp nerves arise in corresponding positions, the main palp nerve $vpn_4$ has a ventral and a dorsal root, and the dorsal root of the circumoesophageal connectives is much smaller than the ventral root. However, there are only three palp nerves, which means, that the nerves $vpn_2$ and $vpn_3$ very likely have been lost; furthermore, there is only one dorsal nerve and the posterior ganglionic expansions of the brain are unknown in the other taxa. The nuchal nerve probably also has a different position,

Source : MNHN, Paris

though the nuchal nerves may have different positions in the Spionida as well (ORRHAGE, 1964, SCHLÖTZER-SCHREHARDT, 1987). The most exceptional features are the ganglionic expansions, which are situated in an area occupied by the foregut in *Protodrilus*. Since they are unkown in the other Protodrilida, with a high degree of probability these characters represent autapomorphies of *P. taenioides*.

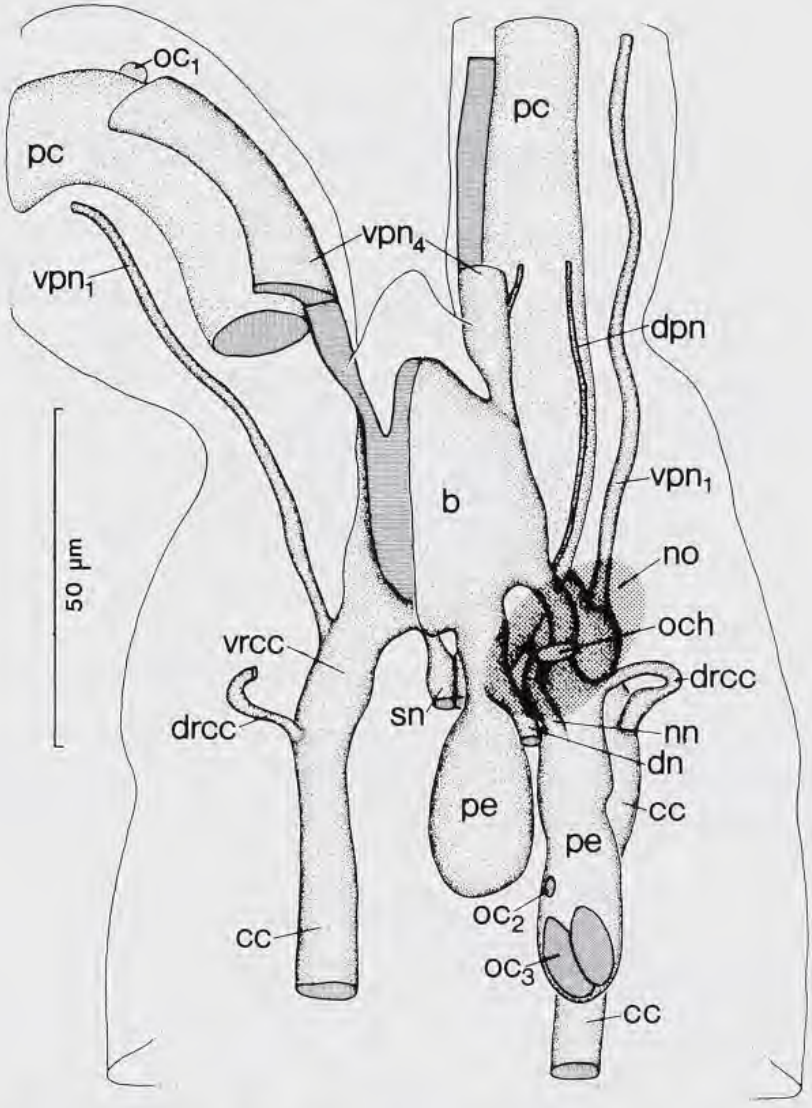



FIG. 4. — *Parenterodrilus taenioides*. Neuropile of the brain (*b*) and associated nerves. Dorsal view; on the left side the dorsal part of the central nervous system has been omitted; reconstruction from electron microscopic observations. *cc* circumoesophageal connective, *dn* dorsal nerve, *dpn* dorsal palp nerve, *drcc* dorsal root of *cc*, *nn* nuchal nerve, *no* nuchal organ, $oc_{1, 2, 3}$ presumed type-1, type-2 and type-3 ocelli; *och* olfactory chamber, *pc* palp canal, *pe* posterior ganglionic expansion of brain, *sn* stomatogastric nerve, $vpn_{1, 4}$ ventral palp nerve 1,4, *vrcc* ventral root of *cc*.

In conclusion, the present findings on *P. taenioides* corroborate its presumed relationship with the other Protodrilida. Its sister group relationship to *Protodrilus* can be sustained by newly found synapomorphies: loss of the ampullae of the palp canals and presence of tentacular phaosomes. Several additional autapomorphies clearly show the derived position of *P. taenioides*: e.g., coelenchyme cells present outside the palp canal, loss of podocytes in the canal, brain with posterior ganglionic expansions, loss of the palp nerves $vpn_2$ and $vpn_3$ and loss of the pigmented ocelli. Other characters are likely to be plesiomorphies and allow a better understanding of the relationship of the Protodrilida.

Source : MNHN, Paris

## REFERENCES


DAUER, D.M., 1987. — Systematic significance of the morphology of spionid palps. *Bull. Biol. Soc. Wash.*, **7** : 41-45.

EAKIN, R.M., MARTIN, G.G. & REED, C.T., 1977. — Evolutionary significance of fine structure of archiannelid eyes. *Zoomorphologie*, **88** : 1-18.

EAKIN, R.M. & HERMANS, C.O., 1988. — Eyes. *In*: W. WESTHEIDE & C.O. HERMANS (eds), The ultrastructure of Polychaeta. *Microfauna Mar.*, **4** : 135-156.

FAUCHALD, K. & JUMARS, P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Ann. Rev.*, **17** : 193-284.

JOUIN, C., 1970. — Recherches sur les Protodrilidae (Archiannèlides) : I. Étude morphologique et systématique du genre *Protodrilus*. *Cah. Biol. mar.*, **11** : 367-434.

JOUIN, C., 1979. — Description of a free-living polychaete without a gut: *Astomus taenioides* n. gen., n. sp. (Protodrilidae, Archiannelida). *Can. J. Zool.*, **57** : 2448-2456.

JOUIN, C., 1992. — The ultrastructure of a gutless annelid *Parenterodrilus* gen. nov. *taenioides* (= *Astomus taenioides*) (Polychaeta, Protodrilidae). *Can. J. Zool.*, **70** : 1833-1848.

ORRHAGE, L., 1964. — Anatomische und morphologische Studien über die Polychaetenfamilien Spionidae, Disomidae und Poecilochaetidae. *Zool. Bidr. Uppsala*, **36** : 335-405.

ORRHAGE, L., 1974. — Über die Anatomie, Histologie und Verwandtschaft der Apistobranchidae (Polychaeta, Sedentaria) nebst Bemerkungen über die systematische Stellung der Archianneliden. *Z. Morph. Tiere*, **79** : 1-45.

ORRHAGE, L., 1990. — On the microanatomy of the supraoesophageal ganglion of some amphinomids (Polychaeta, Errantia) with further discussion of the innervation and homologues of the polychaete palps. *Acta Zool. (Stockh.)*, **71** : 45-59.

ORRHAGE, L., 1991. — On the innervation and homologues of the cephalic appendages of the Aphroditacea (Polychaeta). *Acta Zool. (Stockh.)*, **72** : 233-246.

PURSCHKE, G., 1986. — Ultrastructure of the nuchal organ in the interstitial polychaete *Stygocapitella subterranea* (Parergodrilidae). *Zool. Scr.*, **15** : 13-20.

PURSCHKE, G., 1990a. — Comparative electron microscopic investigation of the nuchal organs in *Protodriloides*, *Protodrilus* and *Saccocirrus* (Annelida, Polychaeta). *Can. J. Zool.*, **68** : 325-338.

PURSCHKE, G., 1990b. — Fine structure of the so-called statocysts in *Protodrilus adhaerens* (Protodrilidae, Polychaeta). *Zool. Anz.*, **224** : 286-296.

PURSCHKE, G., 1990c. — Ultrastructure of the "statocysts" in *Protodrilus* species (Polychaeta): reconstruction of the cellular organization with morphometric data from receptor cells. *Zoomorphology*, **110** : 91-104.

PURSCHKE, G., 1992. — Ultrastructural investigations of presumed photoreceptive organs in two *Saccocirrus* species (Polychaeta, Saccocirridae). *J. Morphol.*, **211** : 7-21.

PURSCHKE, G., 1993. — Structure of the prostomial appendages and the central nervous system in the Protodrilida (Polychaeta). *Zoomorphology*, **113** : 1-26.

PURSCHKE, G. & JOUIN, C., 1988. — Anatomy and ultrastructure of the ventral pharyngeal organs of *Saccocirrus* (Saccocirridae) and *Protodriloides* (Protodriloidae fam. n.) with remarks on the phylogenetic relationship within the Protodrilida (Annelida: Polychaeta). *J. Zool. (Lond.)*, **215** : 405-432.

PURSCHKE, G. & JOUIN-TOULMOND, C., 1993. — Ultrastructure of presumed ocelli in *Parenterodrilus taenioides* (Polychaeta, Protodrilidae) and their phylogenetic significance. *Acta Zool. (Stockh.)*, **74** : 247-256..

RHODE, B., 1990. — Ultrastructure of nuchal organs in some marine polychaetes. *J. Morphol.*, **206** : 95-107.

SCHLAWNY, A., GRÜNIG, C. & PFANNENSTIEL, H.-D., 1991. — Sensory and secretory cells of *Ophryotrocha puerilis* (Polychaeta). *Zoomorphology* , **119** : 209-215.

SCHLÖTZER-SCHREHARDT, U., 1987. — Ultrastructural investigations of the nuchal organs of *Pygospio elegans* (Polychaeta). II. Adult nuchal organs and dorsal organs. *Zoomorphology*, **107** : 169-179.

STORCH, V. & SCHLÖTZER-SCHREHARDT, U., 1988. — Sensory structures. *In*: W. WESTHEIDE & C.O. HERMANS (eds), The ultrastructure of Polychaeta. *Microfauna Mar.*, **4** : 121-133.


Source : MNHN, Paris

# Genome size in Polychaetes: relationship with body length and life habit

*R. SOLDI*, L. RAMELLA*, M. Cristina GAMBI***
*Paolo SORDINO** & Gabriella SELLA**

* Department of Animal Biology
University of Turin, via Accademia Albertina 17
10123 Torino, Italy
** Laboratorio di Ecologia del Benthos
Stazione Zoologica "Anthon Dohrn"
80077 Ischia, Napoli, Italy.

## ABSTRACT

Only a few species of polychaetes have previously been analyzed for nuclear DNA content (CONNER *et al.* ,1972), by means of microdensitometric analysis of the amount of Feulgen-stained DNA in interphase nuclei. We have correlated genome sizes of 47 species of Polychaeta with mean body length of adult worms. In the species examined genome sizes ranged from 0.07 to 1.2 pg of DNA per nucleus in interstitial species and from 0.4 to 7.2 pg in macrobenthic species. The lowest values are among the lowest genome sizes of invertebrates so far investigated. Genome size appeared to be significantly correlated with mean body length ($r = 0.30$; $df = 45$; $0.05 < P < 0.01$), which ranged from 0.9 mm to 250 mm in the species we examined.

## RÉSUMÉ

**Taille du génome chez les Polychètes : rapports avec la taille du corps et l'habitat**

Le contenu nucléaire en ADN chez les Polychètes a été jusqu'à maintenant étudié chez très peu d'espèces (CONNER *et al.*, 1972). La taille du génome de 47 espèces de Polychètes a été mesurée à l'aide d'une analyse microdensitométrique de la quantité d'ADN des noyaux en repos colorés par la réaction de Feulgen. Cette taille a été corrélée avec la longueur moyenne du corps des annélides adultes de chaque espèce. La quantité d'ADN haploïde varie de 0,07 à 1,2 pg chez les espèces de la méiofaune et de 0,4 pg à 7,2 pg chez les espèces macrobenthiques. Les valeurs les plus petites sont parmi les plus faibles mesurées chez toutes les espèces d'invertébrés analysées jusqu'à maintenant. La longueur moyenne du corps des espèces examinées est comprise entre 0,9 mm et 250 mm, et est significativement corrélée avec la taille moyenne du génome ($r = 0,30$ ; $df = 45$; $0.05 < P < 0.01$), chez les espèces étudiées.

## INTRODUCTION

Genome size (also known as the C-value) is defined as the mass of DNA in a haploid genome (HINEGARDNER,

SOLDI, R., RAMELLA, L., GAMBI, M.C., SORDINO, P. & G. SELLA, 1994. — Genome size in Polychaetes: relationship with body length and life habit. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 129-135. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

1976). Genome size is known to be positively correlated with cell volume and size, length of cell cycle, duration of meiosis and developmental rates (CAVALIER-SMITH, 1985; MCKINNEY & MCNAMARA, 1991). These correlations are believed not to be a direct function of genome size but to result from a balance between selective forces favoring larger cells, and hence larger genomes, and those favoring rapid cell multiplication (more easily achieved with small cells and small genome sizes).

Very small organisms, such as those in the interstitial marine fauna, have never been examined to test whether these relationships apply. In addition to their small size, interstitial organisms have so many biological and ecological adaptations to life in a harsh and variable environment, such as the sediment interstices, that they can be considered very specialized living forms (WESTHEIDE, 1984).

Among lower invertebrates, polychaetes show the highest variety in body sizes and morphology; this reflects their high diversity of niches and life histories. Their morphological variation is probably due to their plasticity and early evolutionary radiation (FAUCHALD, 1984). Among polychaetes, nine families are exclusively represented by interstitial taxa (WESTHEIDE, 1985, 1990) and many others have interstitial representatives (e.g. Hesionidae, Syllidae, Dorvilleidae). These organisms thus could represent good "biological tools" for studying relationships between genome size, body size and organization. Up to now data on genome size for the Polychaeta are scarce. Only CONNER *et al.* (1972) measured nuclear DNA amounts for several species of polychaetes by means of microdensitometric determinations of Feulgen dye content of somatic nuclei and fluorimetric quantitation of the DNA of sperm cells. However, among the species considered by CONNER *et al.* (1972), there were no interstitial taxa.

This report is a first attempt to test the hypothesis that, in polychaetes, a positive correlation between genome size and body size may be expected, especially when interstitial forms are included in the study.

## MATERIALS AND METHODS

To the 27 species of polychaetes considered by CONNER *et al.* (1972) we added 20 species. They were chosen on the basis of their availability. Among the species considered, 13 belong to the meiofauna and 34 to the macrofauna. Among the interstitial species, three belong to exclusively interstitial families (*Saccocirrus papillocercus*, *Mesonerilla intermedia*, *Dinophilus gyrociliatus*).

Individuals of *O. labronica* and *O. puerilis* were collected in 1991 in the harbour of Genoa (Italy) and individuals of *D. gyrociliatus* were collected in 1992 in the aquarium of Leghorn (Italy). Specimens of *O. robusta* and *O. macrovifera* came from strains set up in 1988 with animals collected in the harbour of Genoa. Specimens of *O. gracilis* came from a strain set up with animals collected at the isle of Sylt (Germany) in 1987, specimens of *O. diadema* came from a collection made in 1989 at Long Beach (U.S.A.), specimens of O. *hartmanni* came from individuals collected in 1990 in Algeciras (Spain). Individuals of *O. l. pacifica* were collected from Woods Hole aquariums in 1984 and individuals of *O. costlowi* from aquariums of Tampa (Florida) in 1986. *O. notoglandulata* individuals came from a 1979 collection in the Sagami Bay (Japan). All these strains of *Ophryotrocha* were kindly provided to us by Prof. B. Åkesson. Individuals of the other species were collected in autumn 1990 and spring 1991 in two coastal biotopes of the island of Ischia (Gulf of Naples, Italy).

The interstitial taxa as well as *P. kefersteini* and *O. flexuosus* (see Table 1) were collected in very coarse sands located at around 8-10 m depth and characterized by a typical "*Amphioxus*-sand" community (PICARD, 1965). The other macrofaunal species (*S. prolifera*, *P. dumerilii*, *A. mediterranea*, *S. spallanzani* and *B. luctuosum*) were collected in very shallow (1-3 m depth) hard bottoms covered by photophylic algae, mainly the brown macroalgae *Cystoseira crinita* and *Halopteris scoparia*. To measure genome sizes, cellular suspensions of whole animals were splashed on cool slides, subsequently air-dried and stained with the Feulgen reaction according to the procedure of ITIKAWA & OGURA (1954). Evaluation of the Schiff-positive material was carried out with a Vickers M86 microdensitometer at a wavelength of 545 ± 5 nm. For absolute DNA calibration mouse sperm and lymphocyte preparations were stained together with polychaete preparations. For each species several slide preparations were obtained with 2 to 20 individuals, according to the availability of live material. At least 50 nuclei per species were measured from different slides (including both spermatozoa and spermatids, when present) except for *O. flexuosus* and *M. intermedia* where only 20 nuclei could be measured. The absorption values obtained as arbitrary units were plotted as percent frequency distribution histograms in order to identify the 1C, 2C, 4C classes of DNA. When the DNA values of sperm were not available, the 1C class value was inferred by halving the 2C class. For the evaluation of absolute DNA amounts, values obtained as arbitrary units were

Source : MNHN, Paris

TABLE 1. — Range and mean of body length (mm) and haploid nuclear DNA content (in pg) by microdensitometric and fluorimetric determination in 47 species of polychaetes. Fluorimetric data are indicated without standard error. * = meiofaunal species; a = present paper; b = CONNER *et al.* (1972).

| Taxa | body length range (mm) | mean body length (mm) | haploid DNA content | SE (%) | reference |
|---|---|---|---|---|---|
| Order Phyllodocida | | | | | |
| Fam. Phyllodocidae | | | | | |
| *Nereiphylla paretti* (Blainville, 1828) | 15-30 | 22.50 | 2.70 | 1.60 | b |
| Fam. Glyceridae | | | | | |
| *Glycera americana* Leidy, 1855 | 150-350 | 250 | 3.50 | 1.90 | b |
| Fam. Hesionidae | | | | | |
| °*Ophiodromus obscurus* (Verrill, 1873) | 13-20 | 16.50 | 1.60 | 9.90 | b |
| *Ophiodromus flexuosus* (Delle Chiaje, 1825) | 35-70 | 58.0 | 0.35 | 0.40 | a |
| Fam. Syllidae | | | | | |
| *Syllis prolifera* Krohn, 1852 | 10-25 | 15 | 0.45 | 2.30 | a |
| Fam. Nereididae | | | | | |
| *Platynereis dumerilii* (Aud. & M. Edws, 1833) | 20-100 | 50 | 1.00 | 3.00 | a |
| *Laeonereis culveri* (Webster, 1979) | 55-75 | 65 | 0.80 | 10.10 | b |
| *Nereis succinea* Frey & Leuckart, 1847 | 80-190 | 130 | 2.20 | 4.00 | b |
| Fam. Nephtyidae | | | | | |
| *Nephtys incisa* Malmgren, 1865 | 25-150 | 80 | 7.20 | | b |
| Fam. Polynoidae | | | | | |
| *Lepidonotus sublaevi* s Verrill, 1873 | 13-34 | 23.50 | 2.20 | | b |
| *Lepidonotus squamatus* (Linnaeus, 1767) | 15-50 | 36 | 1.50 | | b |
| Order Amphinomida | | | | | |
| Fam. Amphinomidae | | | | | |
| °*Linopherus ambigua* (Monrò, 1933) | 47 | 47 | 2.40 | 5.50 | b |
| Order Eunicida | | | | | |
| Fam. Onuphidae | | | | | |
| *Onuphis eremita oculata* Hartman, 1951 | 30-120 | 76 | 1.70 | 6.70 | b |
| *Diopatra cuprea cuprea* (Bosc, 1802) | 50-300 | 170 | 2.00 | 3.00 | b |
| °*Americonuphis magna* (Andrews, 1891) | 150-350 | 250 | 1.20 | | b |
| Fam. Lumbrineridae | | | | | |
| *Lumbrineris tenuis* (Verrill, 1873) | 70-150 | 110 | 2.40 | 6.60 | b |
| *Ninoe nigripes* Verrill, 1873 | 100 | 100 | 5.30 | | b |
| Fam. Dorvilleidae | | | | | |
| **Ophryotrocha hartmanni* Huth, 1934 | 1.8-4.0 | 2.50 | 1.20 | 5.05 | a |
| **Ophryotrocha notoglandulata* Pfannenstiel, 1972 | 2.2-8.0 | 2.50 | 0.36 | 2.90 | a |
| **Ophryotrocha costlowi* Åkesson, 1978 | 2.2-5.0 | 3 | 0.45 | 2.20 | a |
| **Ophryotrocha* sp. *(labronica pacifica)** | 2.2-5.0 | 3 | 0.40 | 2.50 | a |
| **Ophryotrocha diadema* Åkesson, 1976 | 1.5-4.6 | 3 | 0.44 | 1.40 | a |
| **Ophryotrocha labronica* Bacci & La Greca, 1962 | 2.2-4.9 | 3 | 0.44 | 3.00 | a |
| **Ophryotrocha* sp. *(robusta )*** | 2.6-5.2 | 3.50 | 0.40 | 5.60 | a |
| **Ophryotrocha* sp. *(macrovifera )*** | 2.4-5.0 | 3.50 | 0.80 | 2.30 | a |
| **Ophryotrocha gracilis* Huth, 1934 | 2.5-4.0 | 3.50 | 0.40 | 3.70 | a |
| **Ophryotrocha puerilis* Clap. & Meczn., 1869 | 3.0-7.0 | 5 | 0.45 | 2.80 | a |
| *Protodorvillea kefersteini* (McIntosh, 1869) | 10-15 | 12.50 | 0.36 | 3.13 | a |
| Order Orbiniida | | | | | |
| Fam. Orbiniidae | | | | | |
| *Scoloplos rubra* (Webster, 1879) | 70 | 70 | 3.10 | 3.40 | b |
| °*Leioscoloplos fragilis* (Verrill, 1873) | 40-150 | 90 | 2.30 | 4.70 | b |

Source : MNHN, Paris

TABLE 1 (continuation). — Range and mean of body length (mm) and haploid nuclear DNA content (in pg) by microdensitometric and fluorimetric determination in 47 species of polychaetes. Fluorimetri data are indicated without standard error. * = meiofaunal species; a = present paper; b = CONNER *et al.* (1972).

| Taxa | body length range (mm) | mean body length (mm) | haploid DNA content | SE (%) | reference |
|---|---|---|---|---|---|
| Order Chaetopterida | | | | | |
| Fam. Chaetopteridae | | | | | |
| *Chaetopterus variopedatus* (Renier, 1804) | 100-250 | 170 | 1.00 | | b |
| Order Cirratulida | | | | | |
| Fam. Cirratulidae | | | | | |
| *Cirriformia luxuriosa* (Moore, 1904) | 110 | 110 | 3.40 | | b |
| °*Cirriformia grandis* (Verrill, 1874) | 150 | 150 | 0.70 | | b |
| *Cirriformia filigera* (Delle Chiaje, 1828) | 200-250 | 225 | 1.00 | 2.20 | b |
| Fam. Paraonidae | | | | | |
| *Aricidea fragilis* Webster, 1879 | 70-100 | 85 | 4.60 | 2.30 | b |
| Order Ophelida | | | | | |
| Fam. Scalibregmidae | | | | | |
| *Scalibregma inflatum* Rathke, 1843 | 60-100 | 80 | 4.00 | | b |
| Order Capitellida | | | | | |
| Fam. Maldanidae | | | | | |
| °*Axiothella mucosa* (Andrews, 1891) | 70 | 70 | 2.70 | 2.20 | b |
| Fam. Arenicolidae | | | | | |
| *Arenicola cristata* Stimpson, 1856 | 120-250 | 136 | 0.90 | 3.30 | b |
| Order Terebellida | | | | | |
| Fam. Pectinariidae | | | | | |
| *Pectinaria gouldii* (Verrill, 1873) | 20-45 | 32 | 1.30 | 7.20 | b |
| Order Sabellida | | | | | |
| Fam. Sabellidae | | | | | |
| *Amphiglena mediterranea* (Leydig, 1851) | 5-15 | 11 | 0.39 | 1.93 | a |
| *Branchiomma luctuosum* (Grube, 1869) | 20-45 | 34 | 1.20 | 4.34 | a |
| °*Branchiomma crispum* (Kroyer, 1856) | 30-70 | 45 | 1.30 | 1.20 | b |
| *Myxicola infundibulum* (Renier, 1804) | 150-200 | 175 | 3.10 | | b |
| *Sabella spallanzanii* (Gmelin, 1791) | 200-300 | 250 | 0.65 | 3.30 | a |
| Order Dinophilida | | | | | |
| Fam. Dinophilidae | | | | | |
| **Dinophilus gyrociliatus* O.Schmidt, 1857 | 0.7-1.30 | 0.96 | 0.07 | 0.62 | a |
| Order Nerillida | | | | | |
| Fam. Nerillidae | | | | | |
| **Mesonerilla intermedia* Wilke, 1953 | 1-2 | 1.40 | 0.37 | 2.70 | a |
| Order Protodrilida | | | | | |
| Fam. Saccocirridae | | | | | |
| **Saccocirrus papillocercus* Bobretzky, 1871 | 25-30 | 27.5 | 0.54 | 1.50 | a |

° *O. obscurus*, reported as *Podarke obscura* in Conner *et al.* (1972)
° *L. ambigua*, reported as *Pseudeurythoe ambigua* in Conner et *al.* (1972)
° *A. magna*, reported as *Onuphis magna* in Conner *et al.* (1972)
* *O. labronica pacifica*, not yet formally described, Åkesson (1984)
** *O. robusta* and *macrovifera*, not yet formally described, Åkesson (1975)
° *L. fragilis*, reported as *Scoloplos fragilis* in Conner *et al.* (1972)
° *C. grandis*, reported as *Cirratulus grandis* in Conner *et al.* (1972)
° *A. mucosa*, reported as *Clymenella mucosa* in Conner *et al.* (1972)
° *B. crispum*, reported as *Branchiomma nigromaculata* in Conner *et al.* (1972)

Source : MNHN, Paris

converted into picograms, taking the mouse genome size as 3.9 picograms (SPARROW *et al.*, 1972). To calculate the correlation between genome size and organism size, we considered body length as an estimate of body size. We are aware that in polychaetes body length is a simplistic measure of body size, and that not always is this parameter positively correlated with the actual size of the worm (DUCHÊNE, 1982). Besides, body length can greatly change in different populations of the same species according to geographic location (climatic), local environment and trophic conditions, and laboratory conditions in the case of laboratory reared populations. High body length variability in polychaetes notwithstanding, in order to compare our data with those of CONNER *et al.* (1972), we used the body length variable because it was the only size-parameter available from the literature. An indicative mean body length for each of the species considered was estimated by comparing and averaging body length data given by different authors. In Table 1 we reported the range of adult body length values, as well as a mean value obtained by averaging values obtained from literature. For the species in our study, we integrated the literature data with the values obtained by measuring at least 10 adult individuals from sampled populations. For the gonochoric species of the genus *Ophryotrocha* 10 sexually mature males and mature females were considered. In *D. gyrociliatus* only females were measured, in simultaneously hermaphroditic species only sexually mature individuals and in protandric sequential hermaphroditic species, worms were measured when they reached the female phase.

This approach allowed us to assess at least the actual "order of magnitude" of body length reached within each single species.

## RESULTS AND DISCUSSION

Genome sizes expressed as pg of DNA per haploid nucleus and mean body lengths of the species examined by us and by CONNER *et al.* (1972) are listed in Table 1, ranking them by orders and families according to PETTIBONE classification (1982). A total of 47 genome sizes are listed, 10 of which were measured by CONNER *et al.* (1972) with the fluorimetric method. The species examined belong to 23 families and 12 orders and are therefore representative of a broad evolutionary range within the class and of a wide spectrum of life habits, mainly represented by shallow-water species.

Genome sizes varied among species from 0.07 pg to 7.2 pg DNA per nucleus. Such a 100-fold range in genome size is comparable only to the ranges found in insects and teleosts. All other animal classes are much more conservative in their genome sizes (JOHN & MIKLOS, 1987). Some of the genome sizes observed in polychaetes are among the lowest found in invertebrates so far investigated. Only Eutardigrada (REDI & GARAGNA, 1987) and some nematodes (JOHN & MIKLOS, 1987) have the same or smaller amounts of DNA.

Genome size appeared to be significantly positively correlated with body length ($r = 0.30$; $df = 45$; $0.05 < P < 0.01$). However, only 9 % (i.e. $r^2$) of the variation in genome size is explained by its relationship to body length. In the 13 interstitial species included in the sample (*Ophryotrocha* spp., *S. papillocercus*, *D. gyrociliatus*, *M. intermedia*) no significant correlation was observed between genome size and body length, but by their small body size and small genome size, they greatly contributed to the significance of the overall r. If they were excluded, the correlation was no longer significant.

Different and contrasting patterns arise in comparing from an evolutionary view point the DNA content in polychaetes. At the generic level, the10 species of *Ophryotrocha* showed quite homogeneous values, except *O. hartmanni*, as discussed by SELLA *et al.* (1993). Furthermore, *P. kefersteini*, that, like *Ophryotrocha*, belongs to the Dorvilleidae family, showed a comparable value. On the other hand, the three species of the genus *Cirriformia* showed quite different DNA amounts (Table 1). At the family level, the Sabellidae (5 species) demonstrated a high variability in genome size, while the Onuphidae (3 species) and the Polynoidae (2 species) showed more homogeneous values. The species belonging to exclusively interstitial families (*D. gyrociliatus*, *M. intermedia* and *S. papillocercus*) have among the smallest DNA amounts. At the order level, one may note that within the Eunicida, the macrofaunal taxa (Onuphidae, Lumbrineridae) have higher DNA amount than the interstitial ones (Dorvilleidae) (Table 1).

Although the sample of interstitial polychaetes is still quite small, these first results suggest that meiofaunal taxa have on the whole smaller genome sizes than macrofaunal ones.

We speculate that the small genome sizes characteristic of meiofaunal species may be partially correlated, not only with body size (not all the interstitial species have necessarily very small dimensions, e.g. *S. papillocercus*) but also with those biological features deriving from an interstitial life habit, such as progenesis (i.e. retention of

Source : MNHN, Paris

juvenile characters produced by a genetically fixed precocious sexual maturation (GOULD, 1977), short life-span, rapid sexual maturation, rapid cycling of generations, few eggs of large size, and brooding.

These features, which are well documented in *Ophryotrocha* spp., *Dinophilus* spp. and in many other meiofaunal polychaetes (SWEDMARK, 1964; WESTHEIDE, 1984), make up life histories with peculiar mosaics of "r" and "K" selected parameters. One may also speculate that small genome sizes can be a prerequisite to interstitial life.

The above considerations are still quite speculative due to the small amount of data to date available on this subject; further analyses on genome sizes in other species of macrofaunal and meiofaunal polychaetes are necessary to corroborate the hypothesis that interstitial polychaetes have smaller genomes than macrofaunal polychaetes. On the whole, the DNA content in polychaetes showed a wide range of values and a large variability. Such features are common to many other biological properties of this highly diversified group of marine organisms.

## ACKNOWLEDGEMENTS

This research was in part supported by a grant from the Italian M.U.R.S.T. (Progetto Genetica Evoluzionistica). We thank the Centro di Studi per l'Istochimica of the C.N.R. (Pavia) for kindly allowing us to use their instruments and Paola Protto for her technical assistance.

## REFERENCES

ÅKESSON, B. 1975. — Reproduction in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *Pubbl. Staz. zool. Napoli*, **39** Suppl. : 377-398.

ÅKESSON, B., 1984. — Speciation in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *In*: A. FISCHER & H.D. PFANNENSTIEL (eds), Polychaete Reproduction. *Fortschr. Zool.* : 299-316.

CAVALIER-SMITH, T., 1985. — *The Evolution of Genome Size*. John Wiley & Sons, Chichester, NewYork, Brisbane, Toronto, Singapore, 523 pp.

CONNER, W. G., HINEGARDNER, R. & BACHMANN, K., 1972. — Nuclear DNA amounts in Polychaete Annelids. *Experientia*, **28** : 1502-1504.

DUCHÊNE, J.C., 1982. — Problèmes liés à la croissance chez les Annélides Polychètes. *Oceanis*, **3** : 493-504.

FAUCHALD, K., 1984. — Polychaete distribution pattern, or: can animals with Palaeozoic cousins show large-scale geographical patterns ? *In*: P.A. HUTCHINGS (ed.), *Proc. First International Polychaete Conference*, Linnean Society of New South Wales: 1-6.

GOULD, S.J., 1977. — *Ontogeny and Phylogeny*. Belknap Press of Harvard University Press, Cambridge Massachusetts and London U.K., 501 pp.

HINEGARDNER, R., 1976. — Evolution of genome size. *In*: AYALA (ed.), *Molecular Evolution*. Sinauer Assoc. Inc. Sunderland, Massachusetts : 179-199.

ITIKAWA, O. & OGURA, Y., 1954. — The Feulgen reaction after hydrolysis at room temperature. *Stain Technology*, **29**: 13-15.

JOHN, B.& MIKLOS, G.L.G., 1987. — *The Eukaryote Genome in Development and Evolution*. Allen and Unwin, London, 291 pp.

MCKINNEY, M.L. & MCNAMARA, K.J., 1991. — *Heterochrony. The Evolution of Ontogeny*. Plenum Press, New York and London, 437 pp.

PETTIBONE, M., 1982. — Annelida. *In*: S.P. PARKER (ed.), *Synopsis and Classification of Living Organisms*. McGraw Hill, London : 43 pp.

PICARD, J., 1965. — *Recherches qualitatives sur les biocénoses marines des substrats meubles dragables de la région marseillaise*. Thèse. Fac. Sc. Nat. Université d'Aix-Marseille, 160 pp.

REDI, C.A. & GARAGNA, S., 1987. — Cytochemical evaluation of the nuclear DNA content as a tool for taxonomical studies in Eutardigrades. *In*: R. BERTOLANI (ed.), *Biology of Tardigrades. Selected Symposia and Monographs U.Z.I.* Mucchi, Modena, **1** : 73-80.

Source : MNHN, Paris

SELLA, G., REDI, C.A., RAMELLA, L., SOLDI, R., PREMOLI, M.C. — 1993. Genome size and karyotype length in some interstitial polychaete species of the genus *Ophryotrocha* (Dorvilleidae). *Genome*, **36** : 652-657.

SPARROW, A.H., PRICE, H.J. & UNDERBRINK, A.G., 1972. — A survey of DNA content per cell and per chromosome of prokaryotic and eukaryotic organisms: some evolutionary considerations. *In*: J. SMITH (ed.), *Evolution of genetic systems, Brookhaven Symposia in Biology.*, **23**. Gordon and Breach, New York: 451-494.

SWEDMARK, B., 1964. — The interstitial fauna of marine sand. *Biol. Rev.*, **39** : 1-42.

WESTHEIDE, W., 1984. — The concept of reproduction in Polychaetes with small body size: adaptations in interstitial species. *In*: A. FISCHER & H. D. PFANNENSTIEL (eds), Polychaete reproduction. *Fortschr. Zool.*, **29** : 265-287.

WESTHEIDE, W., 1985. — The systematic position of the Dinophiliidae and the Archiannelid problem. *In*: S. CONWAY MORRIS, D. GEORGE, R. GIBSON & H.M. PLATT (eds), *The origin and relationships of lower invertebrates*. Oxford University Press, Oxford : 310-326.

WESTHEIDE, W., 1990. — Polychaetes: interstitial families. *Synop. Brit. Fauna*, **44** : 1-153..

Source : MNHN, Paris

Source : MNHN, Paris

# Fine morphology of the feeding apparatus of *Cossura* sp. (Polychaeta, Cossuridae) from the White Sea

*Alexander B. TZETLIN*

Dept. of Invertebrate Zoology
Moscow State University
Moscow, Russia

ABSTRACT

Morphology of the feeding structures and construction of the anterior part of the body cavity of *Cossura* sp. from the White Sea were studied using TEM and SEM techniques. Buccal tentacles are the only feeding structures in the spacious buccal cavity. They are situated on the dorsal surface of the buccal cavity near the esophageal opening. There are about 15 buccal tentacles covered by long cilia inside the proboscideal cavity. In cross sections every tentacle consists of columnar epithelial ciliated cells and in the central part, inside a ring of basal membrane, there are two longitudinal muscle cells and two cells without contractile filaments. The space between body wall and tissues of digestive tract is occupied by the non-contractile cytoplasmic parts of longitudinal muscle cells of the body wall. Buccal tentacles cannot be protracted by hydrostaic pressure of the body cavity, as there is no free coelomic space either in the anterior part of the body or inside the tentacles. Also *Cossura* sp. has not circular muscles in the body wall which are usually necessary for hydrostatic skeleton. It seems that natural position for the buccal tentacles during feeding processes is partly projected from the very widely open mouth. According to our observations on living specimens, the long unpaired dorsal branchial filament never takes part in feeding, it is always stretched along the trunk, and has presumably a respiratory function.

RÉSUMÉ

**Morphologie fine de l'appareil alimentaire de *Cossura* sp. (Polychète, Cossuridae) de la mer Blanche**

La morphologie des structures trophiques et la constitution de la partie antérieure cavitaire du corps de *Cossura* sp. de la mer Blanche ont été étudiées en utilisant les techniques de miscroscopie électronique à transmission et de microscopie électronique à balayage. Les tentacules buccaux sont les seules structures servant à l'alimentation, présentes dans la vaste cavité buccale. Il y a environ 15 tentacules couverts de longs cils à l'intérieur de la cavité proboscidéale. En coupe, chaque tentacule est constitué par des cellules épithéliales ciliées en forme de colonnes et dans la partie centrale, à l'intérieur d'un anneau de la membrane basale, il y a deux cellules musculaires longitudinales et deux cellules sans filaments contractiles. L'espace entre la paroi du corps et les tissus du tractus digestif est occupé par les parties cytoplasmiques non contractiles des cellules musculaires longitudinales de la paroi du corps. Les tentacules buccaux ne peuvent être développés par la pression hydrostatique de la cavité corporelle, tout comme il n'y a pas d'espace coelomique libre ni dans la partie

TZETLIN, A.B., 1994. — Fine morphology of the feeding apparatus of *Cossura* sp. (Polychaeta, Cossuridae) from the White Sea. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 137-143. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

antérieure du corps ni dans les tentacules. De même, *Cossura* sp. n'a pas de muscles circulaires dans la paroi du corps, lesquels sont habituellement nécessaires pour le squelette hydrostatique. En position naturelle durant les phases d'alimentation, les tentacules buccaux semblent être partiellement projetés hors de la bouche très largement ouverte. Suivant nos observations sur des animaux vivants, le long filament branchial dorsal ne joue aucun rôle dans l'alimentation. Il est toujours accolé le long du tronc et a, probablement, une fonction respiratoire.

## INTRODUCTION

The Cossuridae is one of the most poorly studied polychaete families. We have very nearly no information even about the general anatomy of these worms. In addition there is almost no information about life style and feeding in these animals (FAUCHALD & JUMARS, 1979; FOURNIER & PETERSEN, 1991). THULIN (1921) and later FOURNIER & PETERSEN (1991) described the ciliated "buccal tentacles" of the pharyngeal cavity of *Cossura* as the feeding apparatus of these polychaetes. Up to this time the construction, position in the pharyngeal cavity and functioning of the cossurid mouth parts have remained unknown.

This paper deals with the fine morphology of the feeding structures and the construction of the anterior part of the body cavity of *Cossura* sp. from the White Sea.

## MATERIALS AND METHODS

All material (about 100 specimens) was collected within 20 km of Velikaya Salma Straight (Kandalaksha Bay, the White Sea, 66° 30'N, 33° 30'E), in the depths varying from 20 to 30 m by means of SCUBA.

The White Sea *Cossura sp.* inhabits the upper layer (1-2 cm) of muddy sediment in depths of more than 20 m. Previously, this species was identified as *Cossura longocirrata* Webster & Benedict (TZETLIN,1981), but according to PETERSEN (personal communication) the White Sea animals must be referred to another, possibly new species.

Live worms were examined in the Laboratory of the White Sea Biological Station of Moscow University. The observations on the *Cossura sp.* were made in a small aquarium with a 3 cm sediment layer transferred from the depth of 25 m.

Animals were fixed with 2,5 % glutaraldehyde, buffered with 0,2 M Na-cacodylate buffer (pH = 7,2-7,4) with the addition of 0,131 g sucrose per 1 ml of solution (1 hour) and postfixed with 1 % osmiumtetroxide solution in the same buffer. For SEM observations specimens were critical-point dried after dehydration in an ethanol series and with acetone and then after coating with gold. They were studied with a Hitachi S 405 microscope. For TEM fixed specimens were dehydrated in an ethanol series, treated with acetone and embedded in Epon. Semithin sections were made with glass knifes on a Dupont Ultracut microtome and stained in 1 % toluidine blue. Ultrathin sections for TEM observations were cut on a LKB-3 Ultracut microtome with diamond knife, stained in lead citrate and uranylacetate and then examined with a JEM-100b microscope. More than 50 specimens were studied by light microscopy in living condition, 25 specimens were observed with SEM. Fifteen of them were cut in the sagittal plane by microsurgery knife and the dissected worms examined with SEM. Four specimens (two sagittal and two transverse series) were examined with TEM techniques.

## RESULTS

CONSTRUCTION OF THE FEEDING APPARATUS. — *Cossura* sp. are slender polychaetes of 20-30 mm length, with 50-60 setigers. The T-shaped mouth opening is located in the fissure between two secondary "segments" of the peristomium. The only external appendage on the anterior part of the body is the dorsal branchial filament, which originates from the border between the second and third setigers. The branchial filament bears a longitudinal row of cilia. The inner part of the branchial filament contains longitudinal muscle cells, and two blood vessels. There is also a narrow coelomic space.

The spacious buccal cavity stretches from the anterior border of peristomium to the border between setigers 2 and 3. In the last area is also the junction between foregut and intestine. The extremely short esophagus is represented by short funnel with relatively narrow lumen between stomodeum and intestine (Fig. 1A).

Stomodeal epithelium consists of squamous (1,6 μm) cells rarely covered by short microvilli (Fig. 1B-C; Fig. 3, C-D). A collagenous matrix on the surface of the stomodeal epithelium is poorly developed. There are electron dense secretory spherulae (D =0,5-0,4 μm) in the epithelial cells. The epithelium is underlain by a thin basal

Source : MNHN, Paris

lamina (0,4 µm) and peritoneal cells. The wall of buccal cavity lacks muscle cells (Fig. 1, B-C; Fig. 3, C-D). Epithelial cells in the back region of the stomodeum are covered with cilia (Fig. 1, A, B). These cells are similar to epithelial cells of the esophageal region and anterior part of intestine.

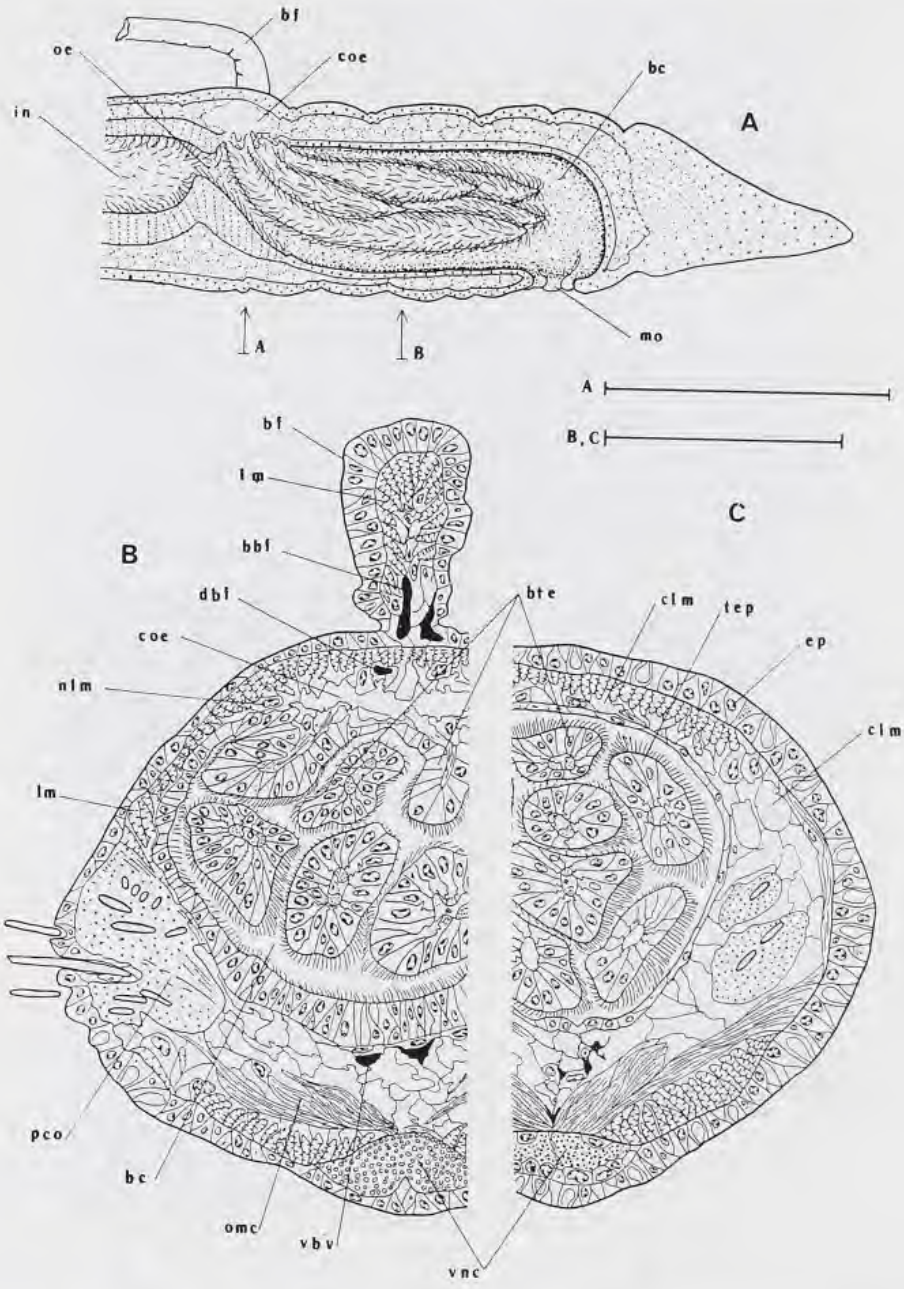



FIG. 1. — *Cossura* sp. **A**. : scheme of sagittal section. Arrows **B, C** show position of transverse sections. **B, C** - transverse sections through the region of the foregut (hemischeme, after TEM-reconstructions). Scale: A - 0,5 mm, **B, C** - 0,1 mm. bc: buccal cavity. bf: branchial filament. bbf: blood vessel of the branchial filament. bte: buccal tentacle. bz: basal zone of the buccal tentacle. c: cilia. ch: chaeta. clm: cytoplasmic expansion of the longitudinal muscle cell. coe: coelomic cavity. dbv: dorsal blood vessel. ep: epitermal epithelium. in: intestine. lm: longitudinal muscle cell. mo: mouth opening n: nucleus. nf: nerve filament. nlm: nucleus of the longitudinal muscle cell. oe: oesophagus. omc: oblique muscle cell. pco: parapodial complex. r: rootlets. step: stomodeal epithelium. sg: secretory granulae. tep: tentacular epithelium. vbv: ventral blood vessel. vnc: ventral nerve cord.

Source : MNHN, Paris

Buccal tentacles, the only feeding structures, are located in the spacious buccal cavity. They are attached to the dorsal surface of the buccal cavity near the opening into esophagus. There are about 15 buccal tentacles covered with long cilia occupying almost all space inside the buccal cavity (Fig. 1, A, B, C). The length of the buccal tentacles is 0,6 - 0,7 mm and the width about 0,05 mm. The ventral and lateral surfaces of tentacles are more densely ciliated than the dorsal surface.

The ciliated epithelium of the buccal tentacles consists of high (20 µm) cells (Fig. 2). Basal bodies and rootlets (with a length of about 18-20 µm) are well developed especially in the epithelial cells placed laterally on the tentacles (Fig. 3, B). Ciliated cells have two types of secretory vesicles: electron dense spherulae (D= 0,5-0,4 µm), the same as in the epithelial cell of the buccal wall. The other type of vesicles (D= 0,8 µm) is full of gray, non-structured serous-like matter. The epithelial cells have large nuclei (D= 5 µm).

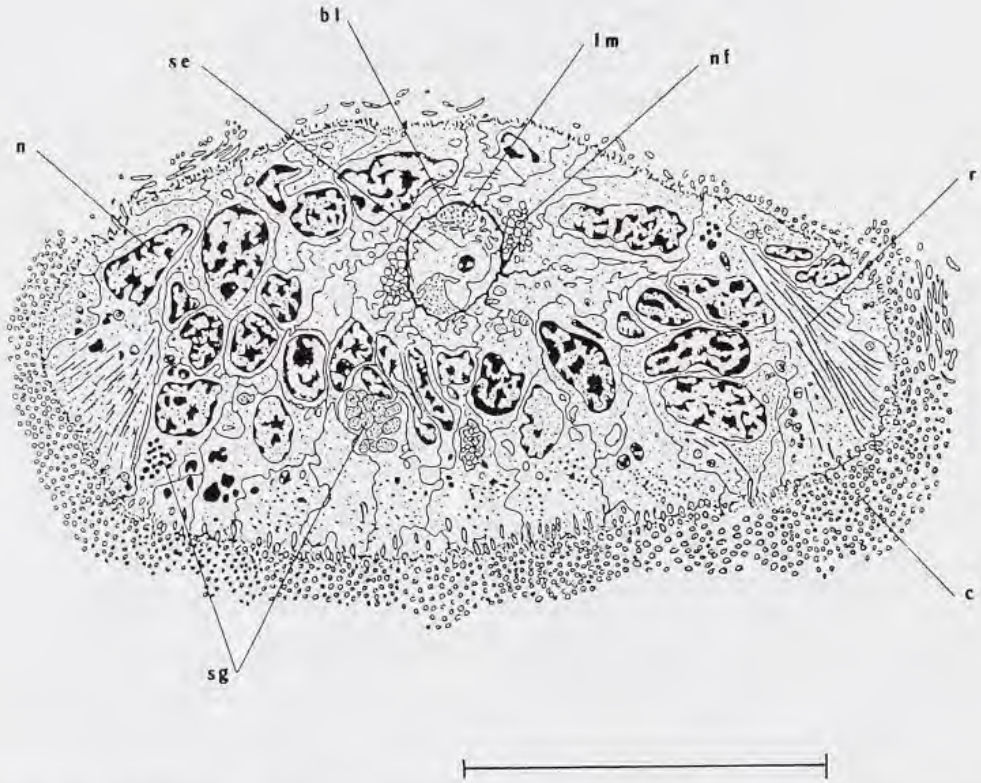



FIG. 2. — *Cossura* sp.: Cross-section of the buccal tentacle (slightly schematic, after TEM-reconstruction). Scale: 0,025mm. For abbreviations, see Figure 1.

The epithelium of the buccal tentacles is underlain by basal lamina (0,16 µm) which rings the central zone. There are two groups of nerve fibres located laterally along the both sides of the basal lamina cylinder.

Transverse sections show two longitudinal muscle cells and two supporting (or coelenchyme-like) cell with almost empty cytoplasm, within the ring of basal lamina. It is possible, that the last structures are only cytoplasmic parts of the muscle cells. The coelomic cavity does not extend into the central cylinder of the tentacles (Fig. 3, A).

CONSTRUCTION OF BODY WALL AND COELOMIC LINING OF THE ANTERIOR END OF THE TRUNK. — There are only longitudinal muscle cells in three bundles (two ventro-lateral and one unpaired dorsal longitudinal bundle) under the ectodermal epithelium and basal lamina. Circular muscles are very poorly developed and could be seen only in the areas of inter-segmental fissures. Oblique muscles are located in the region of the parapodial complexes. All longitudinal muscle cells have a spacious non-contractile cytoplasmic expansion in which the nucleus is found. These cytoplasmic extension occupy all the space of the body cavity in the anterior setigers and fit closely to the peritoneal cells which surrounds the foregut (Fig. 3, C). The little space free of cell bodies is

Source : MNHN, Paris

only in the dorsal region of the third setiger. It is directly connected to the coelomic cavity of the branchial filament.

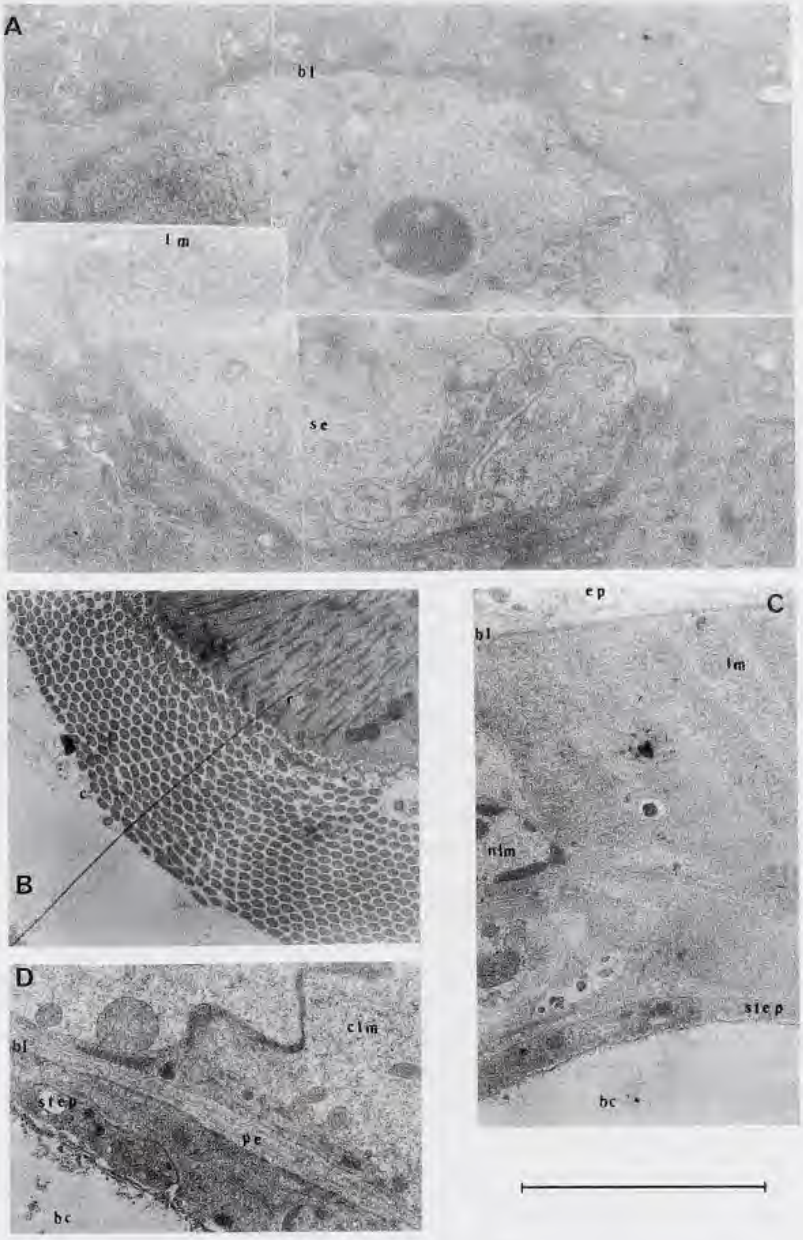



FIG. 3. — *Cossura* sp.: **A**, Central part of buccal tentacle in transverse section (TEM); **B**, ciliated epithelial cell of the buccal tentacle (TEM); **C**, part of a transverse section through anterior part of the body (TEM); **D**, part of the epithelium of the middle part of the buccal cavity (TEM). Scale: **A**, 0.003 mm, **B, C**, 0.014 mm, **D**, 0.0045 mm. For abbreviations, see Figure 1.

LIVING OBSERVATION. — The worms do not build massive tubes, but continuously produce mucus which is always covered with sediment particles. The long dorsal branchial filament never takes part in feeding, being always stretched along the trunk inside the mucous tube presumably having only a respiratory function. After extraction from the sediment the worms usually break up into fragments and die rapidly.

Source : MNHN, Paris

Buccal tentacles are normally located inside the buccal cavity. Only few worms with buccal tentacles extended from the mouth were observed. The tentacles were motionless and non-contractile. All these animals were in bad condition and convulsively contracted the anterior end. These worms were unable to retract their buccal tentacles.

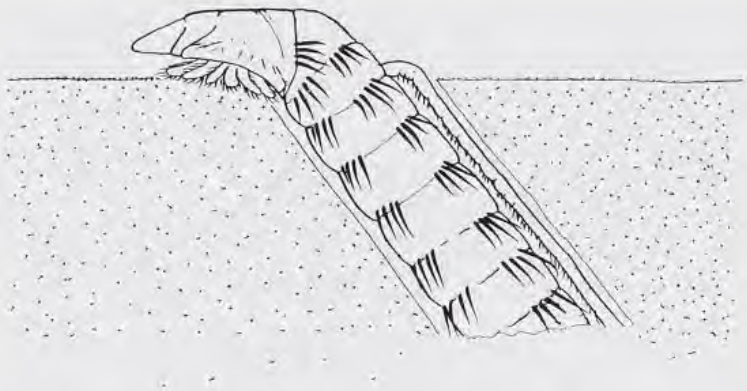


FIG 4. — *Cossura* sp.: Hypothetical position of *Cossura* sp. during feeding processes. For abbreviations, see Figure 1.

## DISCUSSION

The central cylinder of the buccal tentacles of *Cossura* consists of longitudinal muscle elements and supporting (coelenchyme-like) elements. A small coelomic space free from the cell bodies in the dorsal region of the third setiger was found (between the branchial filament and the base of the buccal tentacles), but no coelomic space is present in the buccal tentacles. It is theoretically possible that powerful contractions of the longitudinal body muscles, coupled with a contraction of the branchial filament could cause the extrusion of the buccal apparatus. In a great number of polychaetes, extrusion of tentacular or palpal structures when hydrostatic pressure is used, is strongly correlated with the presence of special compartments of the coelom with muscular walls (ampullae of Spionida, Protodrilidae and Saccocirridae and diaphragms in the Terebellida).

Thus, it is unlikely that contraction of the longitudinal body muscles, coupled with a contraction of the branchial filament may be the normal mechanism of tentacle elongation. It is more probable that the supporting elements of the central cylinder of the buccal tentacles form a kind of chord, supporting the constant shape and volume of the tentacle. Construction of the central cylinder of *Cossura* is similar to the construction of the palpal canal of *Protodriloides chaetifer* (PURSCHKE, 1993). In both cases there are longitudinal muscle elements (without circular elements) and supporting (coelenchyme-like) elements. *P. chaetifer* and *P. symbioticus* differ from other Protodrilida (Protodrilidae and Saccocirridae) by the absence of ampullae and circular muscle in the wall of the palpal canal. Although the diameter of the buccal tentacles of the *Cossura* is twice as large as that of the palp of *Protodriloides*, the number of longitudinal muscle cells in the central cylinder (two in a cross-section) is rather less than in the palpal canal of *Protodriloides* (seven-eight, PURSCHKE, 1993). Considering their structure, the buccal tentacles of *Cossura* must be little movable. So, the tentacles of *Cossura* are not able to move actively along the surface of the substratum and the enormous elongations so typical for tentacles of the Terebellida (SUTTON, 1957). Living observation (unfortunately very limited) also support this conclusion. Protraction of the whole buccal cavity as a component of normal feeding behavior (as suggested by THULIN, 1921 and FOURNIER & PETERSEN, 1991) is hardly probable since we did see observe any system of retractors connected to the tentacles or the foregut. The only possible hypothesis seems to be that the buccal tentacles will be exposed to the substratum when the mouth is opened very wide (Fig. 4). In this case tentacles may be pressed down onto the sediment. The high density of cilia on the lateral and ventral surfaces of buccal tentacles supports this assumption. However, the mechanism of contact of the feeding apparatus of *Cossura* with sediment is not absolutely clear.

From a functional point of view the cossurid tentacular apparatus appears similar to the ciliated pharynx of adult Orbiniidae (FAUCHALD & JUMARS, 1979). In morphological terms, the buccal tentacles of the Cossuridae differ considerably from the tentacular apparatus of the Terebellida both in position and way of action. In the Terebellidae and Alvinellidae tentacles are located on the outer surface of the upper lip, in the Pectinariidae on the

Source : MNHN, Paris

level of mouth opening, and in Ampharetidae the tentacles are on the inner surface of the upper lip of the mouth (FAUVEL, 1897; DALES, 1962, DESBRUYÈRES & LAUBIER, 1986). In contrast, the tentacles of the cossurids are situated on the dorsal surface of buccal cavity near the esophageal opening. The hydrostatic mechanism of tentacle elongation is associated with a special organ in the body cavity of Terbellida, in the form of a muscular diaphragm with paired reservoirs (DALES, 1962; SUTTON, 1957). Such devices are absent in Cossuridae. The ciliated tentacles of Cossuridae may be derived from ciliated structures on the dorso-lateral surfaces of buccal cavity common in a number of different polychaete families (PURSCHKE, 1984, 1985, 1987; TZETLIN, 1991).

## ACKNOWLEDGMENTS

I am grateful to kindness of Mr. Michail SAPONOV and Drs. Oleg MALUTIN, Igor KOSEVITCH and Alexey ELFIMOV for assistance in sampling. I am also grateful to Dr. Mary PETERSEN and Mrs. Marina SAPHRONOVA for fruitful discussions and Drs Kristian FAUCHALD and Don REISH for reviewing the manuscript.

## REFERENCES

DALES, R.P., 1962. — The polychaete stomodeum and the interrelation of the families of Polychaeta. *Proc. Zool. Soc. London*, **139** : 389-428.

DESBRUYÈRES, D., & LAUBIER, L., 1986. — Les Alvinellidae, une famille nouvelle d'annélides polychètes inféodées aux sources hydrothermales sous-marines: systématique, biologie et écologie. *Can. Journ. Zool.*, **64** : 2227-2245.

FAUCHALD, K., & JUMARS, P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. Ann. Rev.*, **17** :193-284.

FAUVEL, P., 1897. — *Recherches sur les Ampharétiens*. Lille, Imp. L. Danel, 230pp.

FOURNIER, J.A., & PETERSEN, M.E., 1991. — *Cossura longocirrata*: redescription and distribution with notes on reproductive biology and a comparison of described species of *Cossura* (Polychaeta, Cossuridae). *Ophelia*, Suppl. **5** : 63 -80.

HOLTHE T., 1986. — Evolution, systematics and distribution of the Polychaeta Terebellomorpha, with a catalogue of the Taxa and a Bibliography. *Gunneria*, **55** : 1-236.

PURSCHKE, G., 1984. — *Vergleichende anatomische und ultastrukturelle Untersuchungen ventraler Pharynx Apparate bei Polychaeten und ihre phylogenetische Bedeutung*. Ph. D. Diss., Gottingen, 372pp.

PURSCHKE., G., 1985. — Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). 2. The pharynx of Nerillidae. *Mikrofauna Mar.*, **2** : 23-60.

PURSCHKE., G., 1987. — Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). 4. The pharynx and jaws of the Dorvilleidae. *Acta Zool.*, Stokh., **68** : 85-105.

PURSCHKE., G., 1993. — Structure of the prostomial appendages and the central nervous system in the Protodrilida (Polychaeta). *Zoomorphology*, **113** : 1-20.

SUTTON, M.F., 1957. — The feeding mechanism, functional morphology and histology of the alimentary canal of *Terebella lapidaria* L. Polychaeta). *Proc. Zool. Soc. Lond.*, **129** : 487-523.

THULIN, G., 1921. — Biologisch-faunistische Untersuchungen aus dem Vresund. V1. Über *Cossura longocirrata* Webster & Benedict und über die Rohren von *Disoma multisetosum* Oersted. *Lunds Univ. Ersskr. N.F.*, Avd. 2, Bd.**17**, 10 : 2-15.

TZETLIN, A.B., 1981. — *Fauna and distribution of the polychaetes of the White Sea*. Ph. D. diss., Moscow, 1- 355 (in Russian).

TZETLIN, A.B., 1991. — Evolution of the feeding apparatus in the order Capitellida (Annelida, Polychaeta). *Zool. Zhurn.*, **70** : 10-22 (in Russian).

Source : MNHN, Paris

Source : MNHN, Paris

# Polychaetes of the Family Acoetidae (= Polyodontidae) from the Levant and the Central Mediterranean with a description of a new species of *Eupanthalis*

*M.Nechama BEN-ELIAHU* & Dieter FIEGE ***

*The Life Sciences Collections, The Department of Evolution, Systematics and Ecology
The Alexander Silberman Institute of Life Sciences
The Hebrew University of Jerusalem, 91904 Jerusalem
**Forschungsinstitut und Naturmuseum Senckenberg
Senckenberganlage 25, D-60325 Frankfurt am Main, Germany

ABSTRACT

Five species of Acoetidae are present along the Mediterranean coast of Israel: *Eupolyodontes cornishii* Buchanan, 1894, a new record for the Mediterranean and, probably, only the second finding of this species since its description from the mouth of the Congo River (Africa); *Euarche tubifex* Ehlers, 1887, also found off Sicily; *Polyodontes maxillosus* (Ranzani, 1817), comparatively rare; *Panthalis oerstedi* Kinberg, 1856 found in deeper waters off the Mediterranean coast of Israel than previously recorded; and *Eupanthalis glabra*, n.sp., from Israel and Cyprus. The new *Eupanthalis* species can be distinguished from another Mediterranean species, *E. kinbergi* McIntosh, 1876, by its smooth rather than papillate palps. The relationship of body size and depth, and differences in body size between Levant and central Mediterranean populations are discussed.

RÉSUMÉ

**Polychètes de la famille des Acoetidae de la Méditerranée levantine et centrale avec la description d'une nouvelle espèce du genre *Eupanthalis***

Cinq espèces de la famille des Acoetidae sont présentes le long des côtes méditerranéennes israéliennes : *Eupolyodontes cornishii* Buchanan, 1894 nouvelle pour la Méditerranée et, probablement, retrouvée pour la deuxième fois depuis sa description originale dans l'estuaire du Congo (Afrique); *Euarche tubifex* Ehlers, 1887 également trouvée en Sicile; *Polyodontes maxillosus* (Ranzani, 1817), comparativement rare; *Panthalis oerstedi* Kinberg, 1856 trouvée plus profondément que lors des récoltes précédentes; et *Eupanthalis glabra*, n. sp., trouvé en Israël et à Chypre. Cette nouvelle espèce d'*Eupanthalis* se distingue de l'autre espèce méditerranéenne, *E. kinbergi* McIntosh, 1876, par ses palpes lisses dépourvus de papilles. Des relations entre les dimensions du corps et la profondeur de récolte ainsi que les différences de taille entre les populations levantines et celles de Méditerranée centrale sont discutées.

---

BEN ELIAHU, M.N. & D. FIEGE, 1994. — Polychaetes of the Family Acoetidae (= Polyodontidae) from the Levant and the Central Mediterranean with a description of a new species of *Eupanthalis*. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162**: 145-161. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

The present paper reports on aphroditoid polychaetes of the family Acoetidae Kinberg, collected between 1968 and 1991 in the Levant Basin off the Mediterranean coasts of Israel and Sinai, and off Cyprus, and in the central Mediterranean off Sicily. Acoetid scaleworms are among the largest polychaete species. They are characterized by parapodial organs (spinning glands) which produce fibers to build permanent felt-like tubes packed with clay (Fig. 7a). Acoetids are carnivorous and have powerful jaws (Figs 2d,e; 6b; 9b). Some species are rarely recorded. Some penetrate to bathyal depths.

A single worm, belonging to the giant species, *Eupolyodontes cornishii*, was collected off Ashqelon in 55 m by E. GILAT and G. SACHNIN in 1969. The identification to species was made by comparison with the holotype. The recent revision of the family Acoetidae by PETTIBONE (1989) enables an appreciation of the rarity and importance of this find (BEN-ELIAHU & FIEGE, 1991); it appears to be the second record since the holotype was described by BUCHANAN (1894) from the mouth of the Congo River. Recently, J. NUÑEZ has found *E.* cf. *cornishii* off Tenerife (NUÑEZ, pers. comm.).

PETTIBONE's revision (1989) led to recognition of a second, undescribed, Mediterranean species of *Eupanthalis* along the coastal shelves of Israel and Cyprus, and it is described below as *Eupanthalis glabra*, sp. nov.

A gradual accumulation of acoetid material has come from increasingly deeper sampling off the Mediterranean coast of Israel, carried out by different projects and institutions: the joint project "Biota of the eastern Mediterranean and Red Sea" of the Hebrew University of Jerusalem and Smithsonian Institution (H. STEINITZ, F.D. POR and W. ARON [discussed in POR *et al.*, 1972]); the Sea Fisheries Research Station, Haifa (E. GILAT); Tel Aviv University (Ch. LEWINSOHN, M. TOM and B. GALIL); the 'Meteor' V expedition (M. TÜRKAY) obtained some particularly rich samples of Acoetidae (for stations, see WEIKERT, 1988). Subsequent deep sampling cruises of pollution monitoring off the northern Israeli coast carried out by S. PISANTY and D. GOLANI (Israel Department of Fisheries and Hebrew University of Jerusalem, respectively); and B. GALIL (The Israel Oceanographic and Limnological Research, Ltd.), have occasionally brought up *Panthalis oerstedi* (BEN-ELIAHU, 1990; BEN-ELIAHU *et al.*, 1991). The combined data provide depth distribution profiles of these species along the Mediterranean coast of Israel.

Recently, the 'Poseidon' 172–4 expedition of the Geologisch–Paläontologisches Institut und Museum, Univ. Kiel to presumed hydrothermically active sites off Sicily (PUTEANUS, 1990), collected *Euarche tubifex*.

## MATERIALS AND METHODS

The samples: samples are listed in Table 1; for Levant sites, see fig. 1 and for Sicilian sites see PUTEANUS, 1990. Abbreviations in the sample codes are as follows: (I) Israel or Cyprus. (TAU) Tel Aviv University; (SFR) Sea Fisheries Research Station, Haifa; (SLMB) sample of "Biota of the Red Sea and eastern Mediterranean" (POR *et al.*, 1972); (SMF) Senckenberg–Museum, Frankfurt; (GPK) Geologisch–Paläontologisches Institut und Museum, Univ. Kiel; (IOLR) Israel Oceanographic and Limnological Research, Co., Ltd.

Repository of specimens is as follow: I-coded material is at the Hebrew University of Jerusalem (HUJ); S-coded material is at the Senckenberg Museum, Frankfurt (SMF). Also, (AMS) Australian Museum, Sydney; (BMNH) Natural History Museum, London; (MNHNP) Muséum National d'Histoire Naturelle, Paris; and (USNM) National Museum of Natural History, Washington.

Measurement of preserved specimens: for population length comparisons, we used H+10 (the prostomium and tentacular segment plus following 10 setigerous segments), which enabled using fragmented as well as complete specimens as suggested by K. FAUCHALD (pers. comm.).

The following data were recorded: (1) Condition of specimen: complete/ anterior fragment/ middle fragment/ posterior fragment; (2) length in mm per number of segments (seg.); (3) length of H+10 in mm; (4) width in mm to edge of parapodia without setae, measured at widest part of body; (5) proboscis length (only if extended) measured from base of prostomium and (6) t, number of teeth on each of the 4 jaws. In addition, for *Eupanthalis glabra*, n. sp., relative length of head appendages, as follows: tentacular cirri/ lateral antenna, tentacular cirri/ palps, lateral antenna/ prostomium, palps/ height of prostomium, tentacular cirri/ height of prostomium, length of proboscis/ height of prostomium; nuchal fold present, absent or not visible due to position of head when preserved.

Source : MNHN, Paris

TABLE 1. — Samples collected off Mediterranean coast of Israel, Cyprus and Sicily

| |
|---|
| 1I-IOLR. Haifa, 33°01'N, 34°34.2'E, L3; 1356 m, beam trawl L3; 5.XI.1990; very rich in rocks and porous metal either volcanic or industrial slag broken up; coll. S. Pisanty & D. Golani. |
| 2I–IOLR. Haifa, L1- 33°02'01"N, 34° 29 E; 1,470 m, L1; 16.XII.1992; coll. B. Galil. |
| 3I-IOLR. Atlit; 200 m, beam trawl; 30.I.1990; coll. B. Galil. |
| 4I-IOLR. Atlit; 500 m, beam trawl; 31.I.1990; coll. B. Galil. |
| 5I-IOLR. Atlit; 1,000 m, beam trawl; 31.I.1990, coll. B. Galil. |
| 6I-SFR1610. Tantura, Gilat st. 17; 110m, dredge A; 3.IV.1968; coll. E. Gilat. |
| 7I-SLMB113. Off Alexander River; 123 m, beam trawl; 26.IX.68, coll. G. Sachnin & M. Rapaport. |
| 8S-SMF. Jaffa, 32°02.38'N, 34°35.05'E — 32°00.95'N, 34°34.52'E,'Meteor' V St. 50; 95-103 m, beam trawl; 26.I.1987; coll. M. Türkay. |
| 9S-SMF. Jaffa, 32°00.53'N, 34°33.98'E,'Meteor' V St. 50; 110 m, grab; 26.I.1987; coll. M. Türkay. |
| 10S-SMF. Jaffa, 32°01'N, 34°31.4'E — 31°58.9'N, 34°27.3'E, "Meteor" V St. 51; 309 m, beam trawl; 26.I.1987; coll. M. Türkay. |
| 11S-SMF. Jaffa, 32°19.96'N, 34°31.46'E - 32°19.75'N, 34°31.26'E, 'Meteor' V St. 56; 694-700 m, beam trawl; 27-28.I.1987; coll. M. Türkay. |
| 12I-TAU. Palmachim; 35 m; 24-26.XI.1977; coll. B. Galil. |
| 13I-TAU. Palmachim; 35 m; 5-6.XI.1987; coll. B. Galil. |
| 14I-SLMB156. Nabi Yunis (Ashdod); 128 m, beam trawl; 20.XII.1968; coll. G. Sachnin & M. Rapaport. |
| 15I-SLMB157. Nabi Yunis (Ashdod); 128 m, dredge B; 20.XII.1968; coll. G. Sachnin & M. Rapaport. |
| 16I-TAU. Nitsanim; 35 m; 28.II.1987; coll. B. Galil. |
| 17I-TAU. Nitsanim; 80 m; 2.IV.1977; coll. B. Galil. |
| 18I-TAU. Nitsanim; 80 m; 1.VII.1977; coll. B. Galil. |
| 19I-SFR1718. Ashqelon; 201 m, beam trawl; 30.X.1968; coll. G. Sachnin. |
| 20I-SFR. 1742-Ashqelon; 55 m, knife dredge; 7.IV.1969; G. Sachnin. |
| 21I-SLMB6046. Sinai, Gaza; 36.6 m, beam trawl; 7.1.70; coll. G. Sachnin. |
| 22I-SLMB6021. el Arish; 137 m, dredge B; 27.VIII.1969, coll. G. Sachnin. |
| 23I-SLMB6023. el Arish; 183 m, dredge B; 24.IX.1969, coll. G. Sachnin. |
| 24I-SLMB6024. el Arish; 183 m, beam trawl, 27.VIII.1969, coll. G. Sachnin. |
| 25I-SLMB178. Sinai, Katib el Galss (Bardawil); 91.5 m, beam trawl; 4.II.1968, coll. E. Gilat. |
| 26I-SLMB1545. Cyprus, Famagusta F; 100-110 m, dredge A; 16.II.1968, coll. A. Lurie. |
| 27S-GPK. Graham Bank, 37°09.135'-37°08.90'N, 12°42.90'-12°43.23'E, "Poseidon" 172-4; 185-178 m, Chain dredge; 2.V.1990; coll. M. Türkay; #645. |
| 28S-GPK. Cimotoe, 37°00.43'-37°00.45'N, 12°39.06'-12°39.11'E, "Poseidon" 172-4; 198-158 m, chain dredge; 7.V.1990; coll. M. Türkay, #718. |
| 29S-GPK. Cimotoe, 37°00.20'-36°059.82'N, 12°39.08'-12°38.58'E, "Poseidon" 172-4; 224-230 m, chain dredge; 2.V.1990; coll. M. Türkay, #629. |
| 30S-GPK. Cimotoe, 36°59.82'-36°058.37'N, 12°39.28'-12°39.90'E, "Poseidon" 172-4; 237- 220 m, chain dredge; 2.V.1990, M. Türkay; #630. |
| 31S-GPK. Cimotoe, 36°059.38'N, 12°38.74'E, "Poseidon" 172-4; 214-230 m, Van Veen grab; 1.V.1990; coll. M. Türkay; #620. |

Statistics were computed by the SAS statistical package. Description of new species gives: holotype parameter (population mean ± s.d. [range], for N, number of individuals). To conform with PETTIBONE (1989), the text refers to segments rather than setigers; in Aphroditoidea the first parapodium bearing setae is the 2nd segment.

Scanning Electron Microscopy (SEM): samples were dehydrated via graded ethanol series, critical–point dried using $CO_2$ and examined in a CAMSCAN–SEM (CS 24).

Source : MNHN, Paris

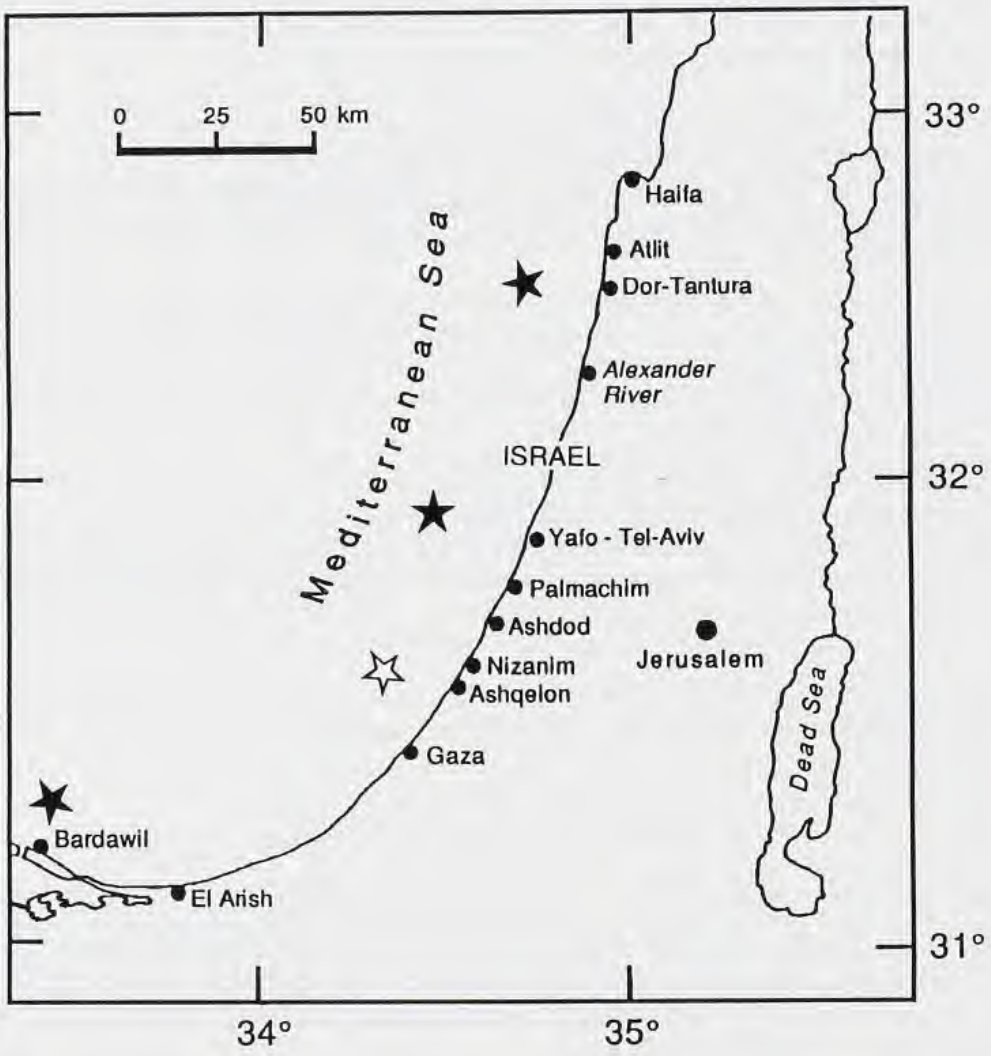



FIG. 1. — Sampling sites off Israel (Haifa to Ashqelon) and northern Sinai (Gaza - Bardawil). Black star, *Eupanthalis glabra*; white star, *Eupolyodontes cornishii*.

Source : MNHN, Paris

## SYSTEMATIC SECTION

### Genus *Eupanthalis* McIntosh, 1876

PETTIBONE, 1989: 24.

### *Eupanthalis glabra*, new species

(FIGS 2-5)

MATERIAL EXAMINED. — Samples: 6I (FIG. 2a); 7I; 8S, Holotype and 66 paratypes; 9S; 14I; 15I; 22I; 23I; 25I; 26I (Table 1). Total: 76 specimens, Cyprus, 1; Israel, 75.

REPOSITORY. — Holotype (HUJ). Paratypes: 23 (HUJ); 24 (SMF 4430); 2 (AMS: W208889, W20890); 7 (BMNH ZB 1992.305–311); 9 (USNM 157612, 157613, 157614); 2 (MNHNP: UC343-A922, 344-A922). Topotype: 1 (SMF 4431).

FIG. 2. — *Eupanthalis glabra*, n. sp.: **a,** anterior end with fully everted proboscis (from Cyprus); **b-e** (from Israeli coast): **b,** anterior end with fully everted proboscis (holotype); **c,** dorsolateral view of anterior end (paratype); **d,** frontal view of proboscis; **e,** lateral view of same. (Scales, **a–e** = 1 mm)

Source : MNHN, Paris

DESCRIPTION. — Body elongate. Largest, complete specimen, 65 mm, 64 seg.; H+10, 2.3 mm; width, 3.5 mm. Holotype (Figs 2b, 3a–j) anterior fragment with pharynx fully extended, 32mm /50 seg. (H+10, 3.0 mm), width 4.0 mm. Population, H+10, 2.8 ± 0.6 mm [2.0- 4.0 mm], N= 20 ; width, 3.5 ± 0.4 mm [2.8-4.0], N= 20.

FIG. 3. — *Eupanthalis glabra*, holotype: **a,** head; **b,** left elytrigerous parapodium from segment 2, anterior view; **c,** left cirrigerous parapodium from segment 3, anterior view; **d,** right parapodium from segment 48, anterior view; **e,** upper neuroseta from segment 2 (1st parapodium); **f,** lower neuroseta of same; **g,** upper neuroseta of segment 3; **h,** middle aristate acicular neuroseta from same; **i,** aristate acicular setae with subdistal tuft from segment 10; **j,** capillary setae with circlets of spines (type b) from same. (Scales: **a** = 1 mm; **b–d,** 100 µm; **e–j,** 50 µm).

Source : MNHN, Paris

Elytra smooth, elongate-oval, delicate; first pair covering prostomium, second and third covering dorsum, remainder leaving middorsum uncovered. Posterior elytra very delicate, with lateral pouches.

Prostomium oval, bilobed, with median longitudinal groove (Figs 2c; 3a; 4a-b), with two pairs of sessile eyes, anterior pair much larger or only slightly larger than posterior pair. Lateral antennae with short ceratophores on anterior side of prostomium, with tapered styles, 1.7 (1.7 ± 0.3 [1.3-2.2], N=17) times longer than prostomium. Palps ventro-lateral to antennae, stout, tapered, smooth, 5.0 (3.4 ± 0.9 mm [2.2-5.3 mm], N=19) times longer than prostomium (Figs 2a-c; 3a).

*First* (tentacular) *segment* distinct dorsally; nuchal lobe observed on holotype (Figs 3a, 4b); tentaculophores lateral to prostomium, each with aciculum, without setae, with dorsal and ventral tentacular cirri subequal in length, 2.2 (2.2 ± 0.4 [1.6-3.3], N= 20) times longer than prostomium, 1.3 (1.3 ± 0.3 [1.0-2.1], N= 17) times longer and stouter than lateral antennae, and 0.4 (0.7 ± 0.2 [0.4-1.0], N= 19) shorter than palps (Figs 2a-c; 3a; 4b).

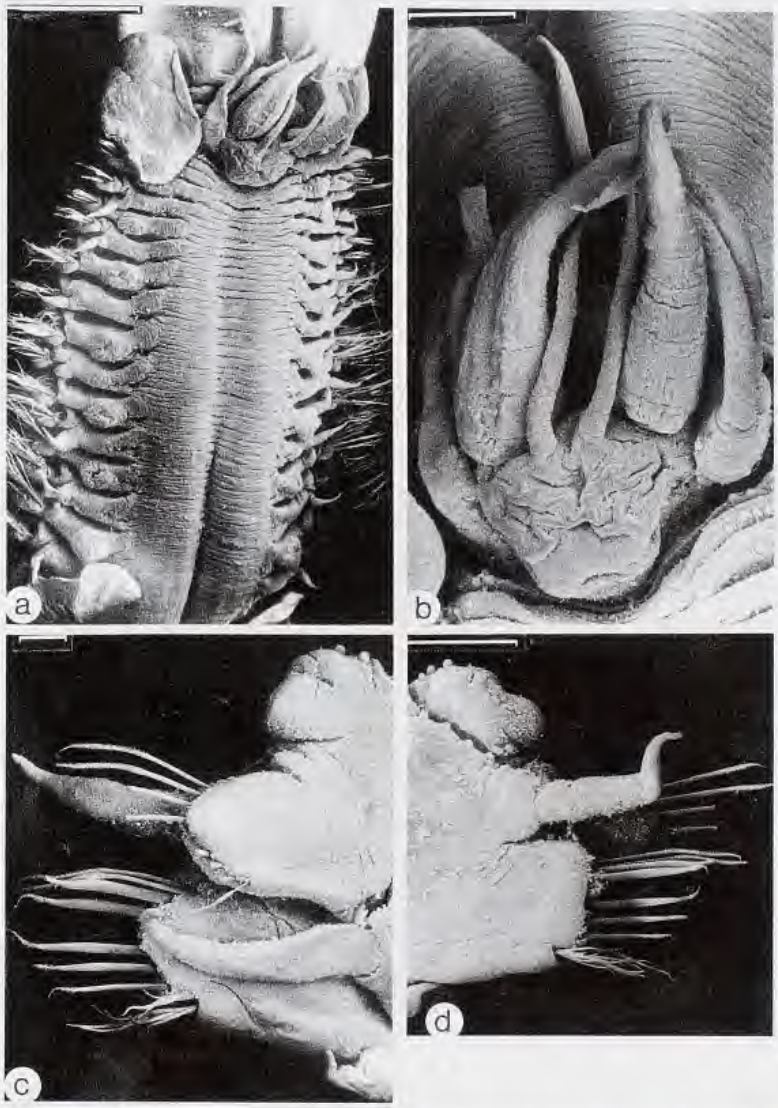



FIG. 4. — *Eupanthalis glabra*, scanning electron micrographs: **a,** anterior end, dorsal view. **b,** same, view more frontal. **c,** right parapodia of segments 2 and 3, anterior view. **d,** right parapodium of segment 3 , posterior view. (Scales: **a** = 1000 µm; **b, d** = 300 µm; **c** = 100 µm).

*Second segment* (first setiger) with first pair of elytrophores; parapodia modified, paw-like, sometimes directed anteriorly, with ventral buccal cirri similar to tentacular cirri, 2.5-3 (N= 2) times longer than following ventral cirri

Source : MNHN, Paris

(Figs 3b-c; 4c-d); notopodium small, rounded acicular lobe on anterodorsal side of larger neuropodium; neuropodium without notosetae, with bilobed presetal acicular lobe.

Extended proboscis 6.9 (7.3 ± 1.8 [5.2-10.3], N=19) times longer than prostomium (Figs 2a-b-e). Distal border of proboscis with 13 pairs of conical papillae, middorsal and midventral ones very slightly enlarged both on wide bases with lateral curved tips (Fig. 2d-e); two pairs of strong honey-colored hooked jaws, each with 2-6 teeth (holotype with 4,3,3,3 teeth), with opposite pattern of dentition in upper left and lower right jaws *vis a vis* lower left and upper right jaws (Figs 2d-e).

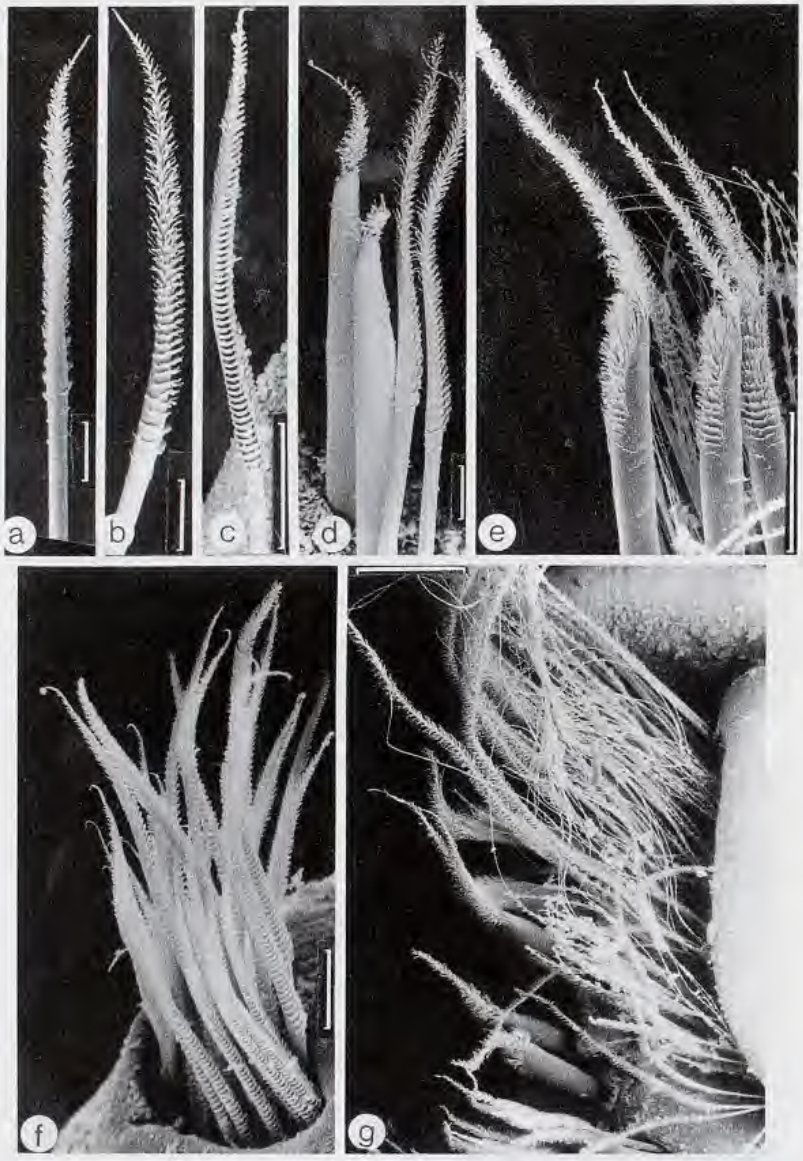



FIG. 5. — *Eupanthalis glabra*, scanning electron micrographs: **a–c**. Neurosetae of segment 2: **a**, upper, posterior view; **b**, same, anterior view; **c**, lower, anterior view; **d**, neurosetae of segment 3: left, middle aristate acicular; right, upper lanceolate; **e**, neurosetae of segment 10: left, middle aristate acicular with subdistal brush; right, upper, type b capillary; **f**, lower neuroseta of segment 4; **g**, setae of segment 10 from anterior, showing fine fibers of spinning gland. (Scales: **a–d**, **f** = 30 µm; **e**, **g** = 100 µm).

Dorsal cirrus on segment 3 with short cirrophore on posterodorsal side of notopodium, with long tapered style, 1.7-2.3 (N= 4) times height of parapodium, 1.8-2.3 (N= 2) times longer than ventral cirrus (Figs 3c; 4c-d).

Source : MNHN, Paris

Beginning with segment 9, notopodium wider, rounded flattened, on anterodorsal side of neuropodium, with internal spinning glands. Middle parapodia with dorsal cirri short, slightly shorter than height of parapodium, 1.5 times shorter than tapered ventral cirri (Fig. 3d).

Far posterior region with notopodia reduced to conical lobes; neuropodia more elongate, narrower, cirri longer than in anterior region. Integument of posterior region very thin. Parapodial branchial tubercles (as in Fig. 8a) not present. Pygidium small, rounded, between few posterior small segments with two anal cirri.

Notosetae present from segment 9 to 19-22, very fine setae with one spiny margin emerging from lower side of notopodium (Fig. 5g). Neurosetae show some anterior–posterior transition in anterior–most parapodia. Neurosetae in three groups (upper with shafts above aciculum; middle with shafts above and below aciculum; lower with shafts below aciculum). Upper neurosetae of two types: *type a* longer, slender, somewhat lanceolate with spinous margins (Figs 3e, g; 5a-b-d), present throughout body; increasingly finer and longer posteriorly (in segment 2 ca. 1.7 times thicker than in segment 3); *type b* very fine, shorter, with circlets of few widely spaced spines (Figs 3j; 5e), lacking in anterior and posterior parapodia.

Middle neurosetae acicular with tips slightly hooked, bearing distal hairy aristae, on segments 3-8 without subdistal tufts of spines (Figs 3h; 5d); from segment 9 on with subdistal tuft (Figs 3i; 5e).

Lower neurosetae curved, with proximal spines on one margin, tapering distally to circumferential, close-set spines (Figs 3f; 5c-f).

*Second segment* (first setiger, Figs 3b; 4c): upper neurosetae, somewhat lanceolate with spinous margins, more massive than in following parapodia, 6 (6-7, 6.3 ± 0.6, N= 4 [Figs 3e; 5a-b]). Lower, 6 (1-6, 3.5 ± 2.1, N= 4 [Figs 3f; 5c]).

*Third segment* (Figs 3c; 4d): upper neurosetae, 2 (1-2, 1.8 ± 0.4, N= 5), 0.3 (0.3-0.6) times as thick as in 2nd segment (Figs 3g; 5d, right). Middle aristate acicular neurosetae, 6 (5-6, 5.6 ± 0.5, N= 5, lacking subdistal spines (Figs 3h; 5d, left), 2.2 (4) times as thick as upper. Lower neurosetae, 35 (14-35, 18.4 ± 9.3, N= 5 [Figs 3c. 4d], with fine shafts ca. 1/4 those of upper neurosetae.

*From and including segment 9*: upper neurosetae, *type a*, 18 [13-21, 16.4 ± 2.9] N= 7); *type b*, 31 [25-42, 32.1 ± 5.5] N=7 (Figs 5e-g). Middle acicular neurosetae with subdistal spines, 7 [1-7, 5.7 ± 1.9, N= 6] (Figs 3i; 5e). Lower neurosetae, 16 [7-16, 12.3 ± 3.3] N= 7 (Fig. 5f).

DISTRIBUTION. — Cyprus (100-110 m), Israel (91.5-183 m [Fig. 1]); note the narrow depth range (Fig. 11).

ETYMOLOGY. — From the Latin, "glaber" meaning smooth, referring to the smooth palps.

REMARKS. — PETTIBONE (1989: 241) redescribed *Eupanthalis kinbergi* according to McINTOSH (1876) and supplemented the description of the holotype, whose palps were missing, with that of a specimen from Naples. McINTOSH did not mention the palps.

As the present material shows, there are two species of *Eupanthalis* in the Mediterranean, one with papillated palps and one with smooth palps. Unfortunately, since the palps are missing on the holotype and not mentioned by McINTOSH, there is no possibility of ascertaining whether or not *E. kinbergi* indeed had papillated palps. We propose that the name *kinbergi* be retained for the species with the papillated palps, as redescribed in PETTIBONE (1989) and the new name, *glabra*, be applied to the Levant species with smooth palps. Another difference between these species is the color of the jaws, dark in *E. kinbergi*, honey-colored in *E. glabra*. *E. glabra* is of much smaller size than *E. kinbergi*. The presence or absence of a nuchal lobe is a difficult character to determine in this preserved material; it appears to be present in *E. glabra* (Figs 2a–c; 3a; 4b).

PETTIBONE (1989) refers to two additional species with smooth palps; *E. edriopthalma* (POTTS, 1910) from the Western Indian Ocean and *E. elongata* (TREADWELL, 1931) from the Philippine Islands; both species have the tentacular cirri about as long as the palps (in *E. glabra*, the tentacular cirri are shorter than the palps); both species lack a nuchal lobe. *E. edriopthalma* has much shorter palps relative to the height of the prostomium than *E. glabra* (syntypes of *E. edriopthalma* with palps 1.1 ± 0.2 [1.0-1.3, N= 2]) times longer than prostomium). Within the type sample containing 67 individuals, the *E. glabra* population showed considerable variability in the relative lengths of the head appendages (length of palps *vis a vis* the antennae and the tentacular cirri, see Figs 2a–c). It may also be related to the degree of contraction when preserved. None of the 19 individuals measured showed the short condition as in *E. edriopthalma*.

*E. elongata* has different neurosetae on segment two and dark jaws (PETTIBONE, 1989). It also has longer antennae relative to the prostomium [N= 1]; only one of 19 specimens of *E. glabra* measured showed the long condition as in *E. elongata*.

Source : MNHN, Paris

The present study points to the difficulty of comparing populations in which variability has been found with species descriptions based on few specimens. This problem is particularly acute in deep-water species with sparse material.

## *Euarche tubifex* Ehlers, 1887

(FIGS 6; 8e)

*Euarche tubifex* - PETTIBONE, 1989: 14-18, Fig. 15.
*Eupanthalis kinbergi* - FAUVEL, 1923: 100-101, Figs. 38i-q; AMOUREUX, 1976: 1049
[Not *Eupanthalis kinbergi* McIntosh, 1876]

MATERIAL EXAMINED: samples: 3I, 3x; 8S; 12I; 13I; 16I; ?16I, 3x; 17I; 21I; 27S, 1x (SMF 4428); 28S, 1x (SMF 4427); 29S, 4x (SMF 4426); 30S, 2x (SMF 4429); 31S (SMF 4425) (Table 1).

Total: 11 specimens from Israel, H+10 length, 5.5 ± 2.2 mm [3-10 mm], N= 9). Largest, AF, 78 mm, 69 segments (H+10, length, 10 mm); width, 9 mm (from sample I12). Nine specimens from Sicily, H+10 length, 9.00 ± 1.32 mm [8-11 mm], N= 9). Largest, AF, 85 mm, 63 segments (H+10, 11mm); width, 15 mm; with eggs.

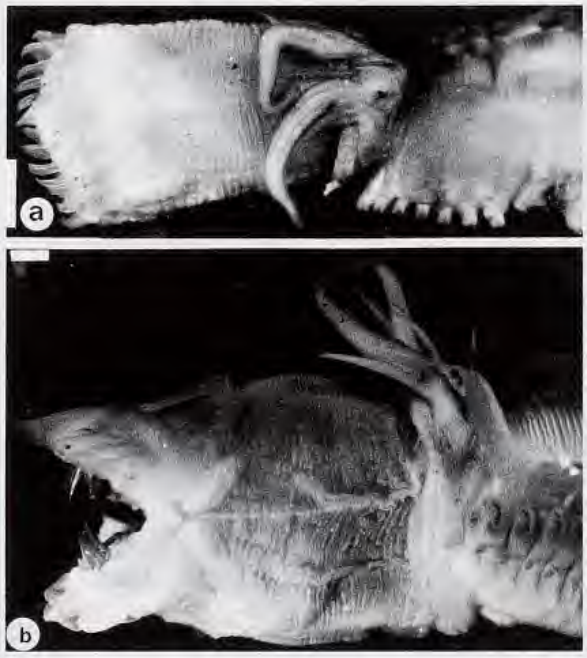



FIG. 6. — *Euarche tubifex*: **a**, specimen from Israel, dorsal view of anterior, proboscis fully extended; **b**, specimen from Sicily, lateral view of same. (Scales: **a**, **b** = 1 mm)

REMARKS. — A decapod belonging to the family Pandalidae (M. TÜRKAY, pers. comm.) was removed from the gut of a Sicilian specimen.

DISTRIBUTION. — Sicily (158-237 m), Israel (35 - 200 m). Worldwide (PETTIBONE, 1989): Caribbean, Northwest Atlantic from Florida to North Carolina, Gulf of Mexico, Panama (Pacific), Southwest Atlantic to South Brazil, Northeast Atlantic from West to Northwest Africa, Mediterranean, Arabian Sea, 13 to 450 m.

Source : MNHN, Paris

## *Eupolyodontes cornishii* Buchanan, 1894

(FIGS 1; 7; 8a–c)

*Eupolyodontes cornishii* Buchanan 1894: 438, pl. 227: Figs 1-8. - PETTIBONE, 1989: 36, Figs 20-22.

MATERIAL. — Sample 20I (Table 1). Anterior fragment, 74 setigers, 230 mm (H+10, 22.7 mm); width, 27.8 mm, fragment of tube. Permanent mounts HUJ-#361, 367; SMF–SEM #30.

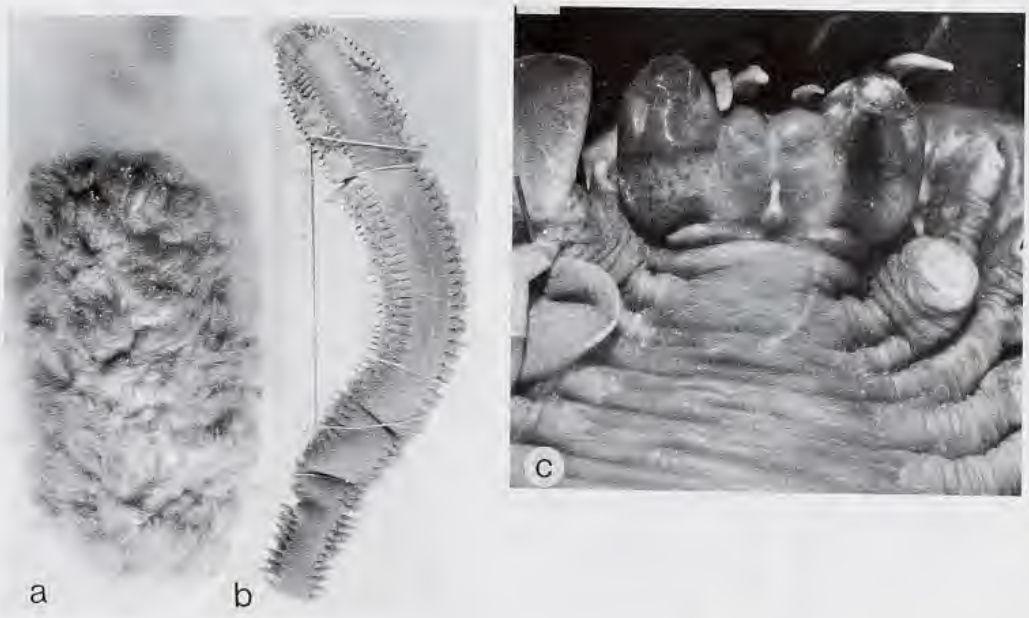



FIG. 7. — *Eupolyodontes cornishii*: **a**, tube after washing out interwoven clay; **b**, anterior fragment, dorsal view, with most elytra missing; **c**, anterior end, dorsal view, with left 1st elytrum pinned back, 1st right elytrum missing. (Scale: **c** = 1 mm).

ADDITIONAL MATERIAL STUDIED. — Africa, off Congo River, 79–86 m, holotype (BMNH 1893.12.8.1).

REMARKS. — The anterior fragment was inside the tube (Figs 7a,b). In her review of the Acoetidae, PETTIBONE (1989) cites only the holotype; she considered another record of a New Caledonia specimen, deposited at the Paris Museum (FAUVEL, 1897) as doubtful. The present material was collected in 1969 (BEN-ELIAHU & FIEGE, 1991) and may be only the second record of *E. cornishii* since that of BUCHANAN in 1894. J. NUÑEZ has recently found *E.* cf. *cornishii* from Tenerife from 200 m depth, based on a fragment of some middle setigers (J. NUÑEZ, pers. comm.).

There are some minor differences from the holotype redescribed by PETTIBONE, mainly in characters which fall within species variability; the description was based on a single specimen. The palps are short, but subequal in length to the ventral tentacular cirri, and slightly surpass the prostomium. Notosetae were observed on the tentacular segment and on segment 2 but not on segments 3 and 4.

Parapodial branchiae begin on segment 8 (rather than 6); most branchiae are simple, some with one branch (Y-shaped. Fig. 8a), fewer with double-Y or with single and Y, best-developed between segments 17-31, and continuing to the end of the fragment. The upper neurosetae (Fig. 8c, cf. Fig 22Ba of PETTIBONE, 1989) show a slight swelling ("neck") at the proximal tuft and are somewhat recurved distally. This was confirmed on the holotype.

Source : MNHN, Paris

DISTRIBUTION. — Israel (55 m). Worldwide (BUCHANAN, 1894): Africa, mouth of Congo River, 35m from land, 79–86m; Tenerife, (200 m) (NUÑEZ, pers. comm.) (55 – 200 m).

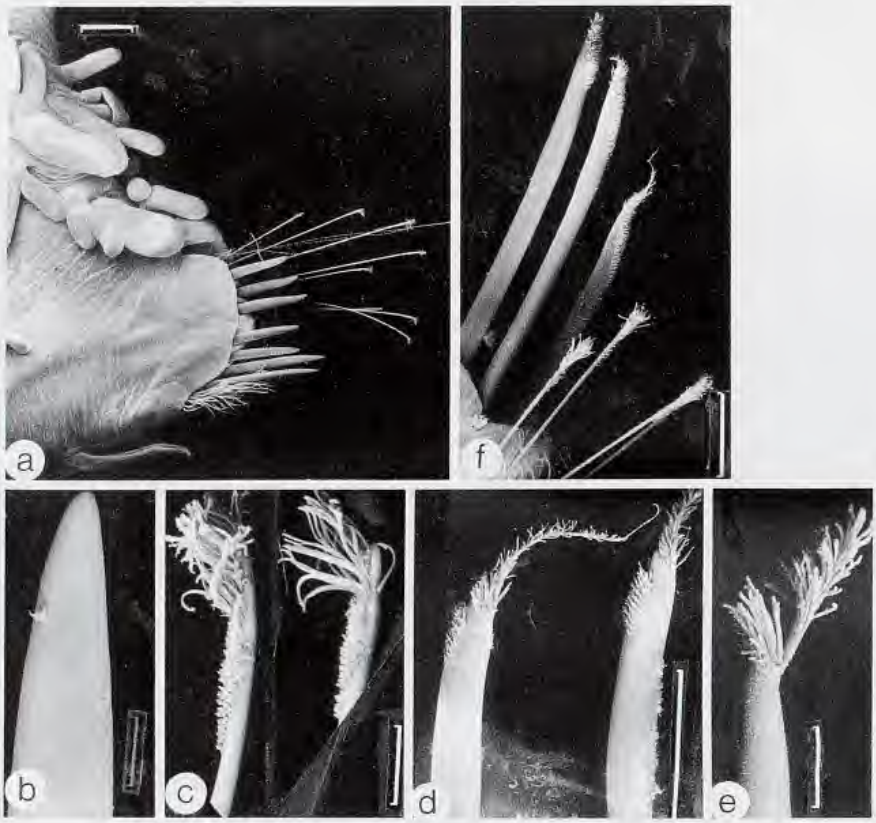



FIG. 8. — Scanning electron micrographs: **a–c**, *Eupolyodontes cornishii*: **a**, 20th right parapodium, posterior view; note parapodial branchiae; **b**, middle acicular neuroseta; **c**, upper neurosetae; **d**, *Polyodontes maxillosus*, middle acicular neurosetae; **e**, *Euarche tubifex*: middle acicular neuroseta from 3rd segment, anterior view; **f**, *Panthalis oerstedi*, tip of 9th right neuropodium, left, middle acicular neurosetae; right, upper neurosetae. (Scales: **a** = 1,000 µm; **b–d**, **f** = 100 µm; **e** = 60 µm).

## *Panthalis oerstedi* Kinberg, 1856

(Figs 8f; 9a–c)

*Panthalis oerstedi* Kinberg, 1856: 387 - PETTIBONE, 1989: 53-56, Figs 32-34; BEN-ELIAHU *et al.*, 1991: 62-64.

MATERIAL EXAMINED. — Samples 1I; 2I; 3I; 4I, 5x; 5I, 6x; 8S, 1x (SMF 4407); 10S, 6x (SMF 4417); 11S, 8x (SMF 4418) ; 19I, 10x; 23I; 24I, 4x (Table 1). Total: 44 specimens, largest, anterior fragment, 18mm, 32 segments, H+10, 5 mm; width, 6.2 mm. Large complete specimen, 35 mm, 71 segments (H+10= 5.5); width 5 mm. H+10, 2.5 - 5.5 mm [3.6 ± 0.8], N= 41.

Source : MNHN, Paris

REMARKS. — Body broadens after about segment 16 and then narrows. Many individuals of sample 5I with opaque dark brown bodies in body cavity, presumably parasites (Figs 9a,c). Figure 9c shows the long filament of the spinning gland in the body cavity. The depth range is extented to 1,470 m.

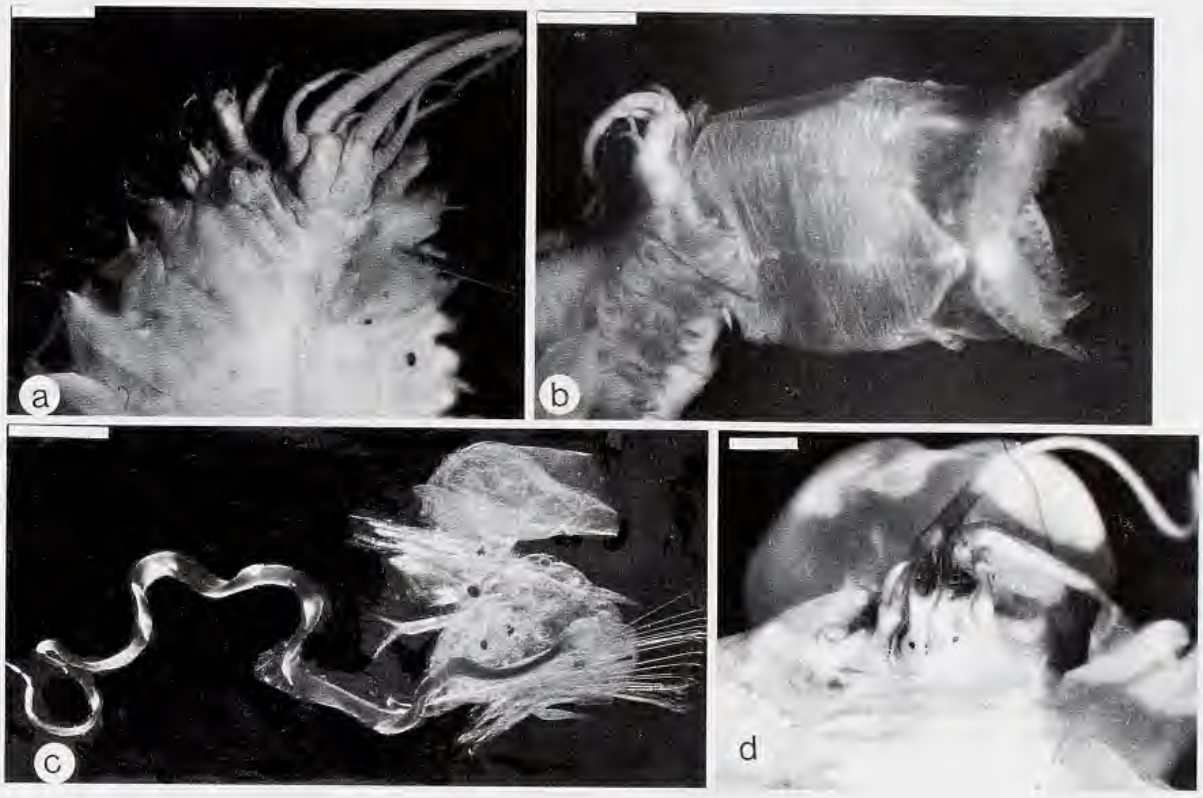



FIG. 9. **a-c.** — *Panthalis oerstedi*; **a,** dorsal view of anterior; **b**, lateral view of anterior end with proboscis fully extended; **c**, parapodium with elytron and long filament of spinning gland in body cavity; dark circles presumed to be cysts of parasite; **d.** *Polyodontes maxillosus*: dorsal view of anterior end. (Scales: **a–d** = 1 mm).

DISTRIBUTION. — Israel (95 m - 1470 m). Worldwide (PETTIBONE, 1989: 56): Sweden, Norway, North Atlantic to Mediterranean, Northwest Africa (11 -760 m); the depth range is broad, 11 – 1,470 m.

## ***Polyodontes maxillosus*** (Ranzani, 1817).

(Figs 8d; 9d)

*Polyodontes maxillosus*. — PETTIBONE, 1989: 101–103, Figs 70–72.

MATERIAL EXAMINED. — Samples 6I; 8S (SMF 4421); 12I (Table 1). Total: three specimens, largest, anterior fragment, 43 mm, 52 segments (H+10, 5 mm); width, 3 mm. H+10, 3.6-5 mm [(4.2 ± 0.7) N= 3).

Source : MNHN, Paris

DISTRIBUTION. — Israel (35-110 m). Worldwide (PETTIBONE, 1989): North Atlantic off Spain, Adriatic, Red Sea, low water to 280 m.

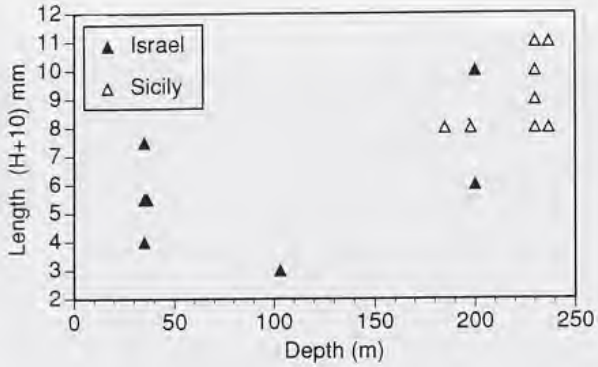



FIG. 10. — Lengths of specimens of *Euarche tubifex* (H+10 parameter) vs. depth.

## KEY TO THE LEVANT ACOETIDAE

1 Eyes stalked (ommatophores); 3 antennae (Figs 7; 9) ..... **2**
Eyes not stalked, sessile; 2–3 antennae (Figs 2a–c; 6) ..... **4**

2 Parapodia branchiae absent (Fig. 9d); palps well–developed (Fig. 9a-d);
acicular neurosetae aristate (Fig. 8d–f) ..... **3**
Parapodial branchiae present (Fig. 8a); palps reduced (Fig. 7c);
neuroacicular; setae not aristate (Fig. 8b); of giant size..... *E. cornishii*

3 Ommatophores white; sessile eyes absent (Fig. 9a);
upper neurosetae penicillate (Fig. 8f) ..... *P. oerstedii*
Ommatophores black; sessile eyes present (Fig. 9d); upper neurosetae
tapered (Fig. 8d) ..... *P. maxillosus*

4 Two antennae (Fig. 2a–c; Fig. 4a-b) ..... **5**
Three antennae (Fig. 6a-b) ..... *E. tubifex*

5 Palps papillated ..... *E. kinbergi* [1]
Palps smooth (Fig. 4a-b) ..... *E. glabra*

## DISCUSSION

Mediterranean biogeographers have reported reduced body size (dwarfing) in several different groups in the Levant marine fauna (sponges, echinoderms, sipunculids and polychaetes [e.g., LAUBIER, 1966]). However, the observation on dwarfing in the Levant has yet to be analyzed properly. The present paper describes differences in length of specimens of *Euarche tubifex* from the Israeli and Sicilian coasts. The Israeli population was of smaller size than the Sicilian one (Israel, H+10, 5.50 ± 2.17 mm [range, 3-10 mm], N= 9, vs. Siciliy, H+10, 9.00 ±

[1] Not found in Levant. Reported from Italy (PETTIBONE, 1989).

Source : MNHN, Paris

1.32 mm [range 8-11 mm], N= 9) and the difference between the means was significant (t-test, t= - 4.1384, p = 0.0008, Fig. 10). Information concerning the age of the specimens is lacking. In addition, the depth ranges sampled may not be comparable: the Israeli *E. tubifex* population came from a broader range, beginning in shallower depths than the Sicilian one (35-200 m : 158-237 m, Israel : Sicily, respectively).

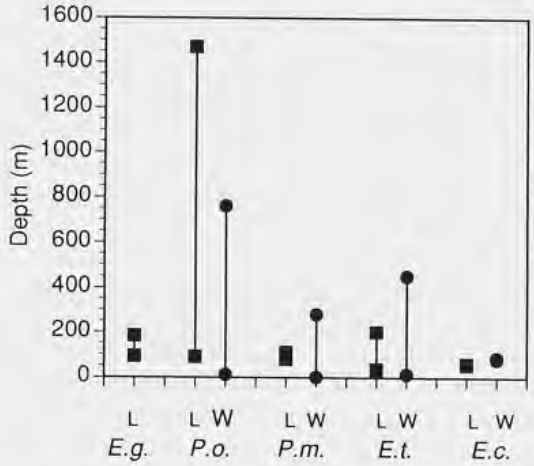



FIG. 11. — Levant (L) and worldwide (W, from PETTIBONE, 1989) depth distribution of acoetid species: E.g., *Eupanthalis glabra*; P.o., *Panthalis oerstedi*; P.m., *Polyodontes maxillosus*; E.t., *Euarche tubifex*; E.c., *Eupolyodontes cornishii*.

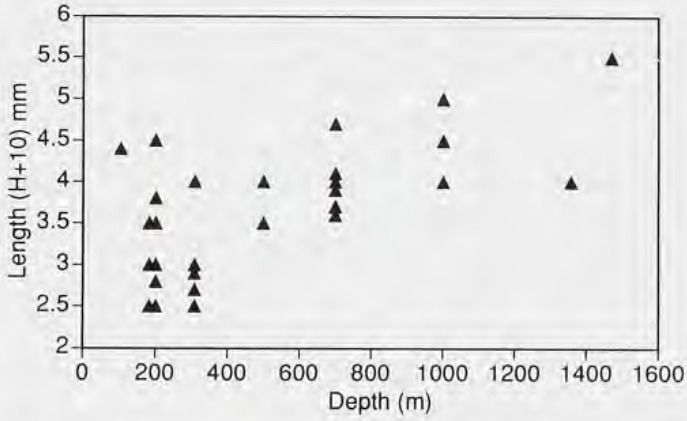



FIG. 12. — Length of specimens of *Panthalis oerstedi* (H+10 parameter) vs. depth.

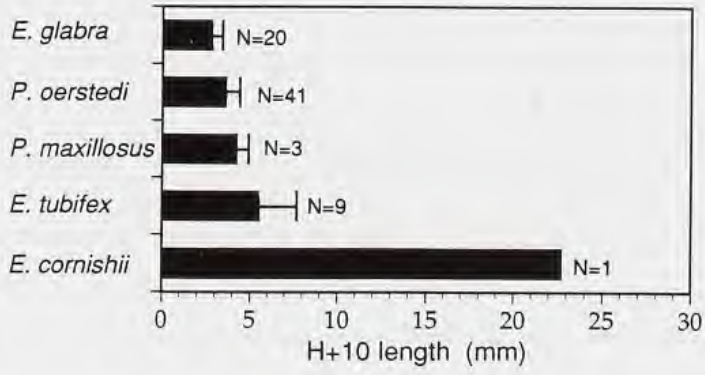



FIG. 13. — Lengths (H+10) of Israeli Acoetidae, mean ± s.d; N, number measured.

Source : MNHN, Paris

To evaluate whether populations from different depths can be compared requires determining whether a positive correlation exists between depth and body size, as in gastropod populations from intertidal and subtidal depths (KOHN, 1971; KOHN & NYBAKKEN, 1975). Two species are rare, *Eupolyodontes cornishii*, found only once, and *Polyodontes maxillosus*, found only three times. One species, *Eupanthalis glabra*, appears to have a very restricted depth range (from 90-183 m, Fig. 11). Thus, the proposed correlations for body size and depth could only be carried out for *Euarche tubifex* (Israel), and *Panthalis oerstedi*.

For *Panthalis oerstedi*, the deepest species (Fig. 11), and one with a great depth range (95 - 1470 m), the Spearman correlation between length of specimens and depth was highly significant (r = 0.60500, p = 0.0001, N= 41, Fig. 12). However, in the Israeli *Euarche tubifex* population, it was *not* significant (r = 0.32154, p= 0.3988, N= 9); the largest specimens were from the greatest depth (Fig. 10), however, the smaller worms were not only from the shallowest depth. The small depth range (165 m) or the small samplesize (N= 9) may contribute to this lack of significance. Unfortunately, on the basis of these results, body sizes of individuals from different *areas* which come from different depths cannot be made.

A comparison of the body sizes of the five Israeli species is given in Fig. 13. Depth distributions of the five species along the Israeli coast are compared with their worldwide distributions given in PETTIBONE, 1989 (Fig. 11). Three of the species' ranges begin in deeper waters in the Levant than elsewhere. This has previously been reported for Levant serpulid species (BEN-ELIAHU, 1991). All four of the smaller species (Figs 11; 13) are present and appear abundant at 100 m. As noted above, the Levant population of *P. oerstedi* is recorded from 1,470 m, 700 m deeper than elsewhere (Fig. 11); the species appears to be abundant from 200 m.

## ACKNOWLEDGEMENTS

We thank M. TÜRKAY of the Forschungsinstitut und Naturmuseum Senckenberg for samples of the 'Meteor' V and the 'Poseidon' 172-4 cruises, and for identifying the decapod prey. Samples were made available by E. GILAT of the Sea Fisheries Research Station; the project, "Biota of the Red Sea and eastern Mediterranean"; the Israel National Collections of Natural History at Hebrew University and at Tel Aviv University for loan of material; S. PISANTY, Department of Fisheries, Ministry of Agriculture; D. GOLANI, The Hebrew University of Jerusalem and B. GALIL, Israel Oceanographic Institute, Ltd.; J. NUÑEZ for data. We also thank D. GATEÑO for assistance with the statistical analysis; S. HALBREICH redrew Figure 3; A. NEEV did some of the photographs. R. BARNICH for French translations; M.L. TRITZ for invaluable assistance. D. GEORGE and A. MUIR for a productive visit to the British Museum (Natural History). H. BROMLEY-SCHNUR, M. TÜRKAY, F.D. POR read previous drafts; two anonymous reviewers made valuable suggestions.

## REFERENCES

AMOUREUX, L., 1976. — *Serpula (Paraserpula) israelitica*, nouvelle espèce de Serpulidae (Annélides Polychètes) et une petite collection annélidienne de la Méditerranée orientale. *Bull. Mus. natl Hist. nat. Paris*, 3 sér., **404** : 1047-1059.

BEN-ELIAHU, M.N., 1990. — Second preliminary report on Polychaeta from some deep-sea benthic sampling in the eastern Mediterranean. Abstract. *In*: Y. MARTH & B. GALIL (eds), *Proc. Second Interdisciplinary Conference on the Continental Shelf of Israel*. Tel Aviv University, May, 1990. Inst. for Nature Conservation Research, Tel Aviv University : 28-29.

BEN-ELIAHU, M.N., 1991. — Red Sea serpulids (Polychaeta) in the eastern Mediterrranean. pp. 515-528. *Ophelia*, Suppl., **5** : 515-528.

BEN-ELIAHU, M.N., M.N. & FIEGE, D., 1991. — Some species belonging to the Aphroditoid family Acoetidae (Polychaeta) from the Levant and the Central Mediterranean. *Abstracts of the Israel Zool. Soc. Meeting*, Dec. 2–3, 1991, Tel Aviv : 11-12.

BEN-ELIAHU, M.N., F.D. POR & B. GALIL, 1991. — A preliminary report on the density and composition of small-size Levantine bathyal benthos. Abstract. *In* : Y. MARTH & B. GALIL (eds), *Proc. Third Annual Symposium on the Mediterranean continental margin of Israel. Israel Ocean.* & Limn. Res., Nat. Inst. Oceanogr. : 62- 64.

BUCHANAN, F., 1894. — A Polynoid with branchiae (*Eupolyodontes cornishii*) *Quart. J. Microsc. Sci.* (Lond.), **35** : 433-450.

FAUVEL, P., 1897. — Observations sur l'*Eupolyodontes cornishii* Buchanan (Annélide Polychète Érrante). *Bull. Soc. Linn. Normandie*, **5** : 88-112.

Source : MNHN, Paris

FAUVEL, P., 1923. — *Polychètes Errantes*. Faune de France **5** : 1-494.

KINBERG, J.G.H., 1856. — Nya slägten och arter of Annelida. *K. Vetensk.–Akad. Förh.*(Stokholm), **12** : 381–388.

KOHN, A.J., 1971. — Diversity and utilization of resources and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. *Limn. Oceanogr.*, **16** : 332-347.

KOHN, A.J. & J.W. NYBAKKEN, 1975. — Ecology of *Conus* on eastern Indian Ocean fringing reefs: diversity of species and resource utilization. *Mar. Biol.*, **29** : 211-234.

LAUBIER, L., 1966. — Sur quelques Annélides Polychètes de la région de Beyrouth. *Am. Univ. Beirut Miscell. Pap.*, **5** : 9-22.

McINTOSH, W.C., 1876. – On the Annelida of the Porcupine Expedition of 1869 and 1870. *Trans. Zool. Soc., Lond.*, **9** : 395-416.

PETTIBONE, M.H., 1989. – Revision of the aphroditoid polychaetes of the family Acoetidae Kinberg (= Polyodontidae Augener) and reestablishment of *Acoetes* Audouin and Milne-Edwards, 1832 and *Euarche* Ehlers, 1887. *Smiths. Contr. Zool.*, **464** : 1-138.

POR, F.D., H. STEINITZ, I. FERBER & W. ARON, 1972. — The biota of the Red Sea and the Eastern Mediterranean (1967-1972). A survey of the marine life of Israel and surroundings. *Isr. J. Zool.*, **21** : 459-524.

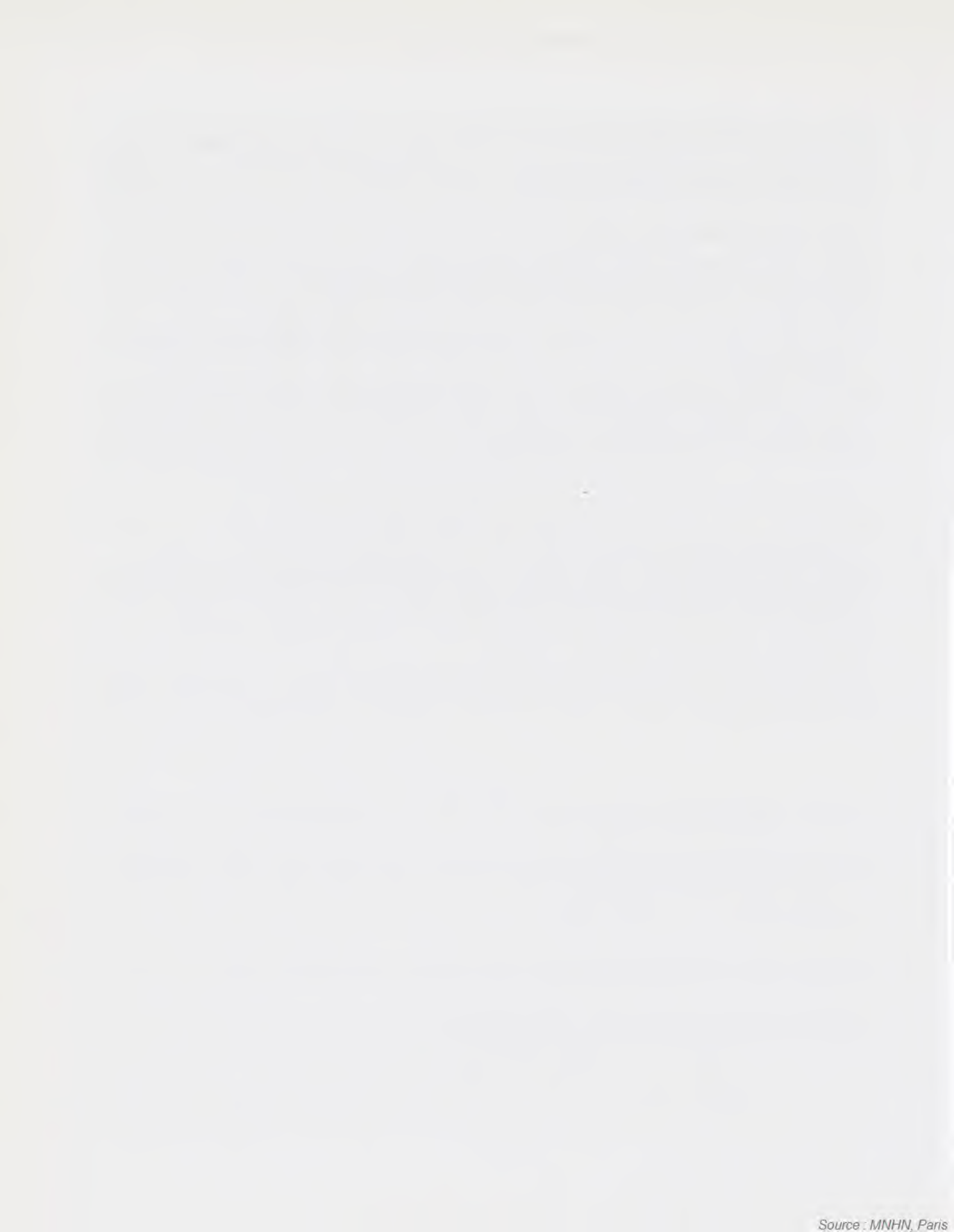
POTTS, F.A., 1910. — Polychaeta of the Indian Ocean, Part 2: The Palmyridae, Aphroditidae, Polynoidae, Acoetidae, and Sigalionidae. *Trans. Linn. Soc., London*, ser. 2, **13** : 325–353.

PUTEANUS, D., 1990. — Cruise Report 'Poseidon' 172–4. MIPAMEHR–MAST I. Volcanism and Hydrothermal Activity in the Strait of Sicily, Malaga – Trapani – Faro, 19.4.–14.5.1990. *Reports, Geol.–Paläont. Inst. Univ. Kiel*, **41** : 1-116.

TREADWELL, A.L., 1931. — Four new species of polychaetous annelids collected by the United States Fisheries Steamer *Albatross* during the Philippine Expedition of 1907–1910. *U.S. Nat. Mus. Bull.*, **100**, 6 : 313–321.

WEIKERT, H., 1988. — Expeditionsbericht über die "Meteor" –Reise 5, Abschnitt 1. (2. Januar bis 28. Januar 1987. Östliches Mittelmeer/ Hamburg – Heraklion – Port Said). Inst. f. Hydrobiologie und Fischereiwissenschaft. *Berichte aus dem Zentrum f. Meeres– und Klimaforschung der Universität Hamburg*: 1-39.

Source : MNHN, Paris



Source : MNHN, Paris

# *Prionospio caspersi* Laubier (Polychaeta, Spionidae) in the Black Sea: long-term monitoring of a population

*Temir A. BRITAYEV*, Alberto CASTELLI** & Tatiana S. AKSIUK**

* A.N. Severtzov Institute of Evolutionary Animal Morphology and Ecology
Russian Academy of Sciences
Leninsky prospect 33, Moscow 117071, Russia
** Istituto di Scienze Antropologiche, Università di Sassari
Corso Margherita di Savoia 15
I-07100 Sassari, Italy

ABSTRACT

Numerous specimens of the spionid polychaete *Prionospio caspersi* Laubier were found in benthic samples from Kapsel Bay, the southeastern coast of the Crimean Peninsula. This was the first record of this species in the Black Sea. *P. caspersi* was very abundant in sandy and silty sand communities at depths of 9 to 23 m. We monitored this community from 1986 to 1991, a period in which the density of *P. caspersi* varied seasonally, being highest in spring (up to 730 ind. $m^2$) and decreasing in the months of August and September (to 96 ind. $m^2$). From April 1986 to April 1989, the frequency of occurrence in grab samples varied from 50 % to 100 %, decreasing at the end of each summer. Interpretation of size-frequency histograms suggests that recruitment took place in the second half of the summer. In autumn 1989 *P. caspersi* disappeared from Kapsel Bay and was not found at the study site or adjacent areas in 1990 or 1991. Possible causes for its disappearance were discussed.

RÉSUMÉ

***Prionospio caspersi* Laubier (Polychaeta, Spionidae) en mer Noire : suivi à long terme d'une population**

De nombreux exemplaires du polychète spionide *Prionospio caspersi* Laubier ont été recueillis sur les fonds de la baie de Kapsel, sur le côtes du Sud-Est de la Crimée, mer Noire. Il s'agit de la première découverte de cette espèce en mer Noire. *P. caspersi* apparaît avec une très grande abondance sur les fonds sableux et sablo-vaseux entre 9 et 23 mètres de profondeur. Nous avons suivi cette communauté de 1986 à 1991, période au cours de laquelle la densité de *P. caspersi* a varié selon les saisons, atteignant au printemps son maximum (jusqu'à 730 ind. $m^2$) et diminuant ensuite dans les mois d'août et de septembre (à 96 ind. $m^2$). D'avril 1986 à avril 1989, sa fréquence dans les échantillons a varié de 50 % à 100 %, diminuant à la fin de chaque été. L'interprétation des histogrammes taille-fréquence suggère que le recrutement advient dans la seconde moitié de l'été. Au cours de l'automne 1989, *P. caspersi* a disparu de la baie de Kapsel, aucun exemplaire n'ayant été retrouvé ni en 1990, ni en 1991. Les causes possibles de cette disparition sont discutées.

---

BRITAYEV, T.A., CASTELLI, A. & T. S. AKSIUK, 1994. — *Prionospio caspersi* Laubier (Polychaeta, Spionidae) in the Black Sea: Long-term Monitoring of a population. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 163- 168. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

*Prionospio caspersi* Laubier, 1962 was first discovered in Venice Lagoon (LAUBIER, 1962) and later found in many areas of the western Mediterranean and Adriatic seas (LAUBIER, 1965; GUÉRIN, 1970). This species inhabits sand and silty-sand sediments of the upper sublittoral zone (LARDICCI, 1989). In the Black Sea, *P. caspersi* was recently found and described from the southeastern coast of the Crimean Peninsula (BRITAYEV *et al.*, 1991, Fig. 1). In this paper we suggested that *P. caspersi* had earlier been misidentified as *P. malmgreni* Claparède, 1868 and that its distribution in the Black Sea was thus probably considerably wider than realized.

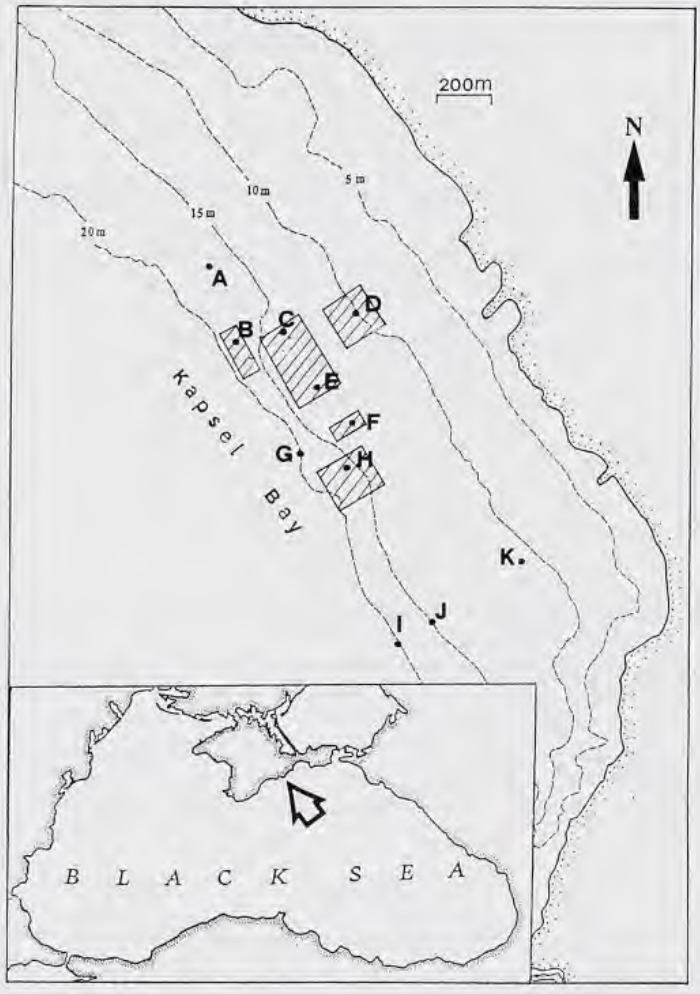



FIG. 1. — Study area in Kapsel Bay, the Black Sea. Sampling stations (A-K) indicated by black dots. Shaded areas show location of mussel (*Mytilus galloprovincialis*) farm.

The ecology of *P. caspersi* in the northern Adriatic, mainly its secondary production in the vicinity of the Po Estuary, was investigated by AMBROGI *et al.*,1985 and AMBROGI, 1990.

During 1986-1991 personnel from the Institute of Fisheries and Oceanology, Moscow, monitored benthic communities in the Black Sea, near Sudak (PERELADOV *et al.*, 1988). During this period benthic samples were collected 2-4 times a year. Since *P. caspersi* was numerically dominant at the study site, the material was suitable for an evaluation of seasonal and long-term changes in the population structure of this species.

Source : MNHN, Paris

## MATERIALS AND METHODS

The study was carried out in Kapsel Bay, near the town of Sudak on the southeastern coast of the Crimean Peninsula, in the area of a mussel (*Mytilus galloprovincialis* Lamarck, 1819) farm (Fig. 1). Benthic samples were collected at the same stations twice a year in 1986-1987 and 1989-1991 (spring and late summer or autumn), and once every three months in 1988. Although not all stations were sampled each time, all sampling periods except November 1990 included samples from within and outside the mussel beds, for the most part about half of each (Table 1). At each station 1-4 samples were taken by a Petersen grab (0.025 $m^2$). The samples were sieved through 0.5 mm mesh and all *P. caspersi* were removed, fixed in a 4 % formalin solution and counted. For study of size-frequency distribution, specimens collected in February, April and August 1988 were used. For each specimen the surface area of the first 10 setigers was calculated according to the method of AMBROGI *et al.* (1985). The material is deposited in the A.N. Severtzov Institute of Evolutionary Animal Morphology and Ecology, Russian Academy of Sciences, Moscow.

## RESULTS

*Prionospio caspersi* inhabited clean fine sand and silty sand at depths of 9 to 23 m in the community of the bivalve mollusc *Chamelea gallina* (L., 1758). At sites where the silty fraction prevailed, *P. caspersi* was absent. It was not found at depths greater than 23 m which may have been the results of the predominance of silty sediments here.

Size-frequency distribution of individuals based on the surface area of the first 10 setigers is shown in Fig. 2. The curves were unimodal in February and April and bimodal in August. The modal area of the first 10 setigers was 0.56 $mm^2$ (average: 0.62 $mm^2$, n = 128 specimens) in February, increasing to 0.71 $mm^2$ (average: 0.76 $mm^2$, n = 146) by April. The first peak of the size-frequency curve in August was formed by individuals with a modal area of 0.34 $mm^2$. This peak reflected the appearance of a new generation. The second peak was formed by specimens with a modal area of 0.64-0.71 $mm^2$. This corresponded to the single peak in winter and spring months formed by specimens of the previous generation. The period from April to August was characterized by negative growth of the population probably reflecting the death of the parent population.

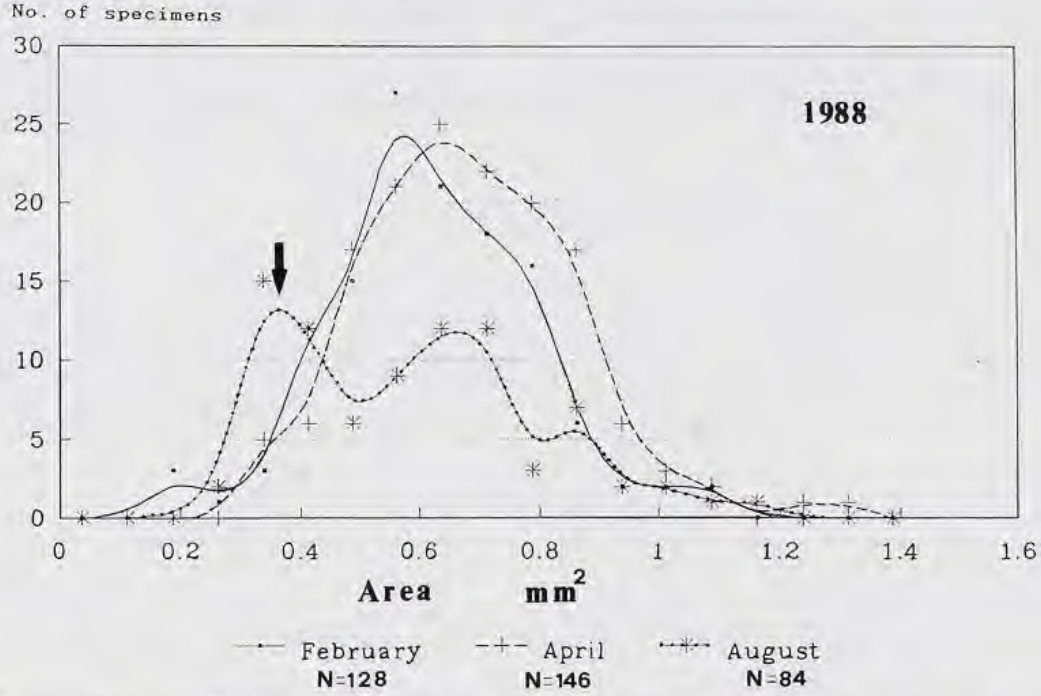



FIG. 2. — *Prionospio caspersi*. Size-frequency curves based on surface area of anterior end calculated according to method of AMBROGI *et al.* (1985). Arrow indicates appearance of recruits.

Source : MNHN, Paris

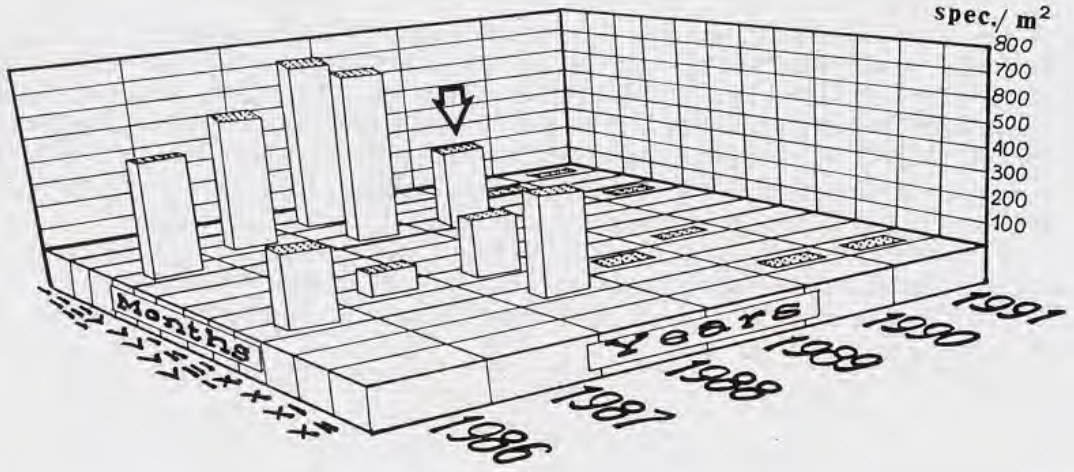



FIG. 3. — *Prionospio caspersi*. Seasonal and long-term changes in population density in Kapsel Bay, Black Sea. Arrow indicates last find of this species.

*Prionospio caspersi* outstripped other benthic species in terms of density and frequency of occurrence in 1986-1988. The maximum density was about 2440 ind.m$^2$, and the mean density varied from 96 to 730 ind. m$^2$.

TABLE 1. — *Prionospio caspersi*. Frequency of occurrence at 11 stations (A-K) in Kapseh Bay, the Black Sea.

| Date | Total number of Petersen grab samples (each 0.025 m$^2$) per station per sampling period/number of samples with *P. caspersi*. Bold stations are ones in mussel beds (see Fig. 1). | | | | | | | | | | | N = Total no. of samples % = Percent frequency of *P. caspersi* in all samples | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A 16m | B 14m | C 12m | D 11m | E 12m | F 15m | G 17m | H 16m | I 22m | J 16m | K 10m | N | % |
| 1986 | | | | | | | | | | | | | |
| Apr. | 4/4 | 2/2 | 1/1 | 1/1 | 3/3 | 3/3 | 1/1 | - | 1/1 | 2/1 | 1/1 | 19 | 95.0 |
| Sep. | 3/2 | 2/2 | 1/1 | 2/2 | 3/3 | 1/1 | 1/0 | - | 1/0 | 3/3 | 1/1 | 18 | 83.3 |
| 1987 | | | | | | | | | | | | | |
| Mar. | 3/3 | 2/1 | 2/2 | 2/1 | 2/2 | 4/3 | 2/2 | 4/3 | 2/2 | 2/2 | 1/1 | 26 | 84.6 |
| Aug. | 2/2 | 2/0 | 4/3 | 2/2 | 2/1 | 4/2 | - | 4/2 | 4/2 | 2/1 | 2/0 | 28 | 53.6 |
| 1988 | | | | | | | | | | | | | |
| Feb. | 2/2 | - | 2/2 | - | 2/2 | - | - | 1/1 | - | 1/1 | - | 8 | 100.0 |
| Apr. | 4/4 | - | 2/2 | - | 4/4 | 2/2 | 2/2 | 4/4 | - | 2/2 | - | 20 | 100.0 |
| Aug. | 4/4 | - | 2/2 | - | 3/3 | 4/4 | 1/0 | 2/2 | 3/3 | 2/2 | 2/1 | 23 | 91.3 |
| Oct. | - | - | - | - | 2/2 | - | - | 2/2 | - | 2/2 | 2/2 | 8 | 100.0 |
| 1989 | | | | | | | | | | | | | |
| Apr. | 2/2 | - | - | 1/1 | 1/0 | - | 2/0 | - | - | 1/0 | 1/1 | 8 | 50.0 |
| Sep. | 1/0 | - | - | 2/0 | 1/0 | 1/0 | 2/0 | 1/0 | - | 1/0 | - | 9 | 0.0 |
| 1990 | | | | | | | | | | | | | |
| Feb. | 1/0 | - | - | - | 1/0 | - | - | - | - | - | - | 2 | 0.0 |
| Aug. | 1/0 | - | - | - | 1/0 | - | - | - | - | 2/0 | - | 4 | 0.0 |
| Nov. | - | - | 1/0 | - | 1/0 | 1/0 | - | 2/0 | - | - | - | 5 | 0.0 |
| 1991 | | | | | | | | | | | | | |
| Jan. | 1/0 | - | 1/0 | - | - | 2/0 | 1/0 | - | 1/0 | - | - | 7 | 0.0 |
| Apr. | 2/0 | - | 2/0 | - | 1/0 | - | - | 2/0 | - | 2/0 | - | 7 | 0.0 |
| Nov. | 1/0 | - | 1/0 | - | - | 1/0 | - | - | - | - | 1/0 | 5 | 0.0 |

Source : MNHN, Paris

In 1988, benthic samples were collected in all seasons, so this year is more suitable than the others for an analysis of the seasonal dynamics of the population. Population density was maximal in winter and spring, decreasing in summer and increasing in autumn (Fig. 3). A decrease of population density in summer was noted also in 1986 and 1987. The decrease in population density in August-September was accompanied by a reduced frequency of occurrence (Table 1).

As a result of benthic community monitoring from 1986 to 1991, the population of *P. caspersi* population may be followed until April 1989 when it was taken for the last time (Fig. 3). *P. caspersi* was absent from samples taken in September 1989 through 1991.

## DISCUSSION

The size-frequency histograms suggest that a recruitment took place in the second part of the summer. These data agree with AMBROGI's (1990) observations. He found that *P. caspersi* had an annual life cycle with intensive recruitment in the beginning of July in the Adriatic Sea. The decrease in density and frequency of occurrence in August-September was probably related with the change of generations. High mortality eliminated the parent population, and at the same time the density of the new generation was low as a result of the prolonged period of recruitment which was not yet over.

The population density of *P. caspersi* in the Adriatic Sea (AMBROGI, 1990) was about 15-20 times higher than in the Black Sea. The trophic conditions in these areas are similar. The concentration of organic carbon in the Black Sea varied from 4.5 to 8.1 $gC.kg^{-1}$ in winter and summer, respectively (PERELADOV, pers. comm.). This is similar to the values found in the Adriatic Sea by AMBROGI (1990) (2.1-8.2 $gC.kg^{-1}$). The sediment structure was similar at both sites. However, the hydrodynamic conditions in the two areas were different. AMBROGI (1990) emphasized the stability of environmental parameters in the Adriatic. In contrast, Kapsel Bay is an exposed bay and the upper layer of sediment is influenced by wave action to 15-20 m, the lower depth of the distribution of *P. caspersi*. This species inhabits the thin upper layer of sediments and is usually disturbed during storms. Therefore, wave action is probably the main factor causing a decrease in the density of *P. caspersi* on the southeastern coast of Crimea.

This theory provides an explanation for the disappearance of *P. caspersi* in the autumn of 1989. In early September 1989 a storm preceded the disappearance of *P. caspersi* (PERELADOV, pers. comm.). In this period the entire population was essentially comprised of young specimens. Destruction of the *P. caspersi* population was probably due to the co-occurrence of this storm with the most vulnerable period of the life cycle. The absence of recruitment in 1990-1991 probably reflected the absence of drift larvae from adjacent areas, i.e., the disappearance of *P. caspersi* in adjacent areas.

## ACKNOWLEDGEMENTS

We are grateful to Mr. M.V. PERELADOV for organizing the monitoring of benthic communities in Kapsel Bay and for fruitful discussion of this paper. We gratefully acknowledge our colleagues Dr. E.G. ZAVARZINA, Mrs. N.V. BRITAYEVA and Mr. M.A. SABURIN for their assistance in collecting and sorting material. We thank Dr. Y.I. KANTOR and Dr. J.A. CHERNIAEV for help with the English and French translations, respectively. We are grateful to Dr. M.E. PETERSEN, whose thoughtful comments improved this manuscript.

## REFERENCES

AMBROGI, R., 1990. — Secondary production of *Prionospio caspersi* (Annelida: Polychaeta: Spionidae). *Mar. Biol.*, **104** : 437-442.

AMBROGI, R., FONTANA, P., & OCCHIPINTI AMBROGI, A., 1985. — Un metodo planimetrico per biometrie di invertebrati marini. Studio preliminare di una popolazione di anellidi policheti. *Nova Thalassia*, **7** (suppl. 3) : 269-274.

BRITAYEV, T.A., CASTELLI, A., & AKSIUK, T.S., 1991. — On the finding of *Prionospio caspersi* (Polychaeta, Spionidae) in the Black Sea. *Zool. Zh.*, **70** : 5-9 (In Russian, English summary).

Source : MNHN, Paris

GUÉRIN, J.-P., 1970. — Description des stades larvaires de *Prionospio caspersi* Laubier (Annélide polychète). Répartition des larves de *Prionospio* en Méditerranée Occidentale. *Tethys*, **2** : 35-40.

LARDICCI, C., 1989. — Censimento dei policheti dei mari italiani. Spionidae Grube, 1850. *Atti Soc. Tosc. Sci. Nat., Mem.*, Serie B, **96** : 121-152.

LAUBIER, L., 1962. — Quelques Annélides polychètes de la lagune de Venise, description de *Prionospio caspersi* n. sp. *Vie & Milieu*, **13** : 124-159.

LAUBIER, L., 1965. — Quelques Annélides polychètes de l'Atlantique récemment signalées ou nouvelles en Méditerranée occidentale. *Rapp. P.V. Comm. Int. Mer Médit.*, **18** : 135-138.

PERELADOV, M.V., BRITAYEV, T.A., ZAVARZINA, E.G., & AKSIUK, T.S., 1988. — The influence of mussel farming on the benthic communities of Sudak Bay (the Black Sea). *Ribnoe Hozaistvo*, **9** : 27-30 (In Russian).

Source : MNHN, Paris

# Systematics, ecology and biogeographical relationships in the sub-family Travisiinae (Polychaeta, Opheliidae)

*Jean-Claude DAUVIN* & Gérard BELLAN***

*Laboratoire de Biologie des Invertébrés Marins et Malacologie, URA CNRS 699
57 rue Cuvier, 75231 Paris Cedex 05, France
**Centre Océanologique de Marseille, URA CNRS 041
Station Marine d'Endoume, rue de la Batterie des Lions, 13007 Marseille, France

ABSTRACT

The Opheliidae is divided into three monophyletic groups corresponding to the three sub-families defined by HARTMANN-SCHRÖDER: Opheliininae, Opheliinae and Travisiinae. The object of the current paper is to offer a contribution to the knowledge of the sub-family Travisiinae including taxonomy, ecology, biogeographical distribution. Three genera are studied: *Dindymenides*, *Kesun* and *Travisia*. Based on previous phenetic and phylogenetic studies of the family and sub-families, we propose to consider *Travisia* as the only valid genus in the sub-family. Twenty-seven species and three sub-species are recognized in this genus. However, many of them are incompletely described and the characters used in species-recognition varies from one author to the next and the validity on some characters has not been recognized until recently. Most of the species must be redefined based on recent findings; we are, however, able to propose a preliminary key to species. Species of *Travisia* general inhabit a muddy substratum, from the intertidal to abyssal depths (7,800 m). Twenty-one taxa are found on the continental shelf and 14 of these are limited to shelf depths (< 200 m). Eleven taxa are found at depths below 2,500 m; three are strictly abyssal. The genus shows a world-wide distribution, but is especially well represented in the Pacific Ocean (21 taxa). Seven taxa are found in the Antarctic Ocean and 10 in the Atlantic Ocean. Sixteen taxa are exclusively to the Pacific Ocean. Eight species with a large geographical range also show extended bathymetric ranges: *T. glandulosa, T. forbesi, T. fusus, T. gravieri, T. japonica, T. kerguelensis, T. olens,* and *T. profundi.* A study of the relationship between species and biogeographical distribution is given.

RÉSUMÉ

**Systématique, écologie et relations biogéographiques dans la sous-famille des Travisiinae (Polychètes, Opheliidae)**

L'ensemble des données sur la famille des Opheliidae a été réuni afin de fournir un état actuel des connaissances sur cette famille. Les Opheliidae se divisent en trois groupes monophylétiques correspondant aux trois sous-famille décrites par HARTMANN-SCHRÖDER : Opheliininae, Opheliinae et Travisiinae. L'objectif de cette note est de fournir une revue des connaissances sur la taxonomie, l'écologie, la distribution biogéographique de la sous-famille des Travisiinae. A partir de considérations phénétiques et phylogénétiques, il est proposé de réunir les trois genres décrits : *Dindymenides*, *Kesun* et *Travisia*, dans le seul genre *Travisia*. Vingt-sept espèces et trois sous-espèces peuvent être reconnues comme valides, cependant beaucoup d'espèces demeurent incomplètement décrites et les caractères morphologiques utilisés changent d'un

DAUVIN, J.C. & G. BELLAN, 1994. — Systematics, ecology and biogeographical relationships in the family Travisiinae (Polychaeta, Ophelidae). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 169-184. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

auteur à l'autre. Bien que la plupart des espèces mérite de nouvelles observations, il est proposé une clé préliminaire d'identification des espèces du genre *Travisia*. Le genre est typique des substrats vaseux, il est rencontré depuis la zone intertidale jusqu'aux abysses (7800 m). Vingt-et-un taxons sont connus du plateau continental, 14 ne dépassant pas ce plateau. Onze taxons ont été recensés à des profondeurs inférieures à 2500 m, trois d'entre eux sont strictement abyssaux. Le genre a une distribution cosmopolite, mais il est particulièrement bien représenté dans l'océan Pacifique (21 taxons). Sept taxons sont antarctiques, 11 atlantiques, 16 sont exclusifs du Pacifique. Huit espèces ont une large distribution géographique et bathymétrique : *T. glandulosa, T. forbesi, T. fusus, T. gravieri, T. japonica, T. kerguelensis, T. olens*, et *T. profundi*. Les relations biogéographiques entre les espèces ont été recherchées.

## INTRODUCTION

During the course of our research, we have had the opportunity to study the species belonging to family Opheliidae, including the genus *Ophelia* (BELLAN & DAUVIN, 1991; BELLAN-SANTINI *et al.*, 1992), and the family in general (BELLAN *et al.*, 1990). In this last paper, the 12 genera of the family were analyzed to attempt a coherent classification of the family. Our results confirm the subdivision into three sub-families originally proposed by HARTMANN-SCHRÖDER (1971): Ophelininae, Opheliinae and Travisiinae. This last sub-family seems particulary suitable to be studied because of the small number of accepted genera: *Dindymenides*, *Kesun* and *Travisia*, its plesiomorphy, and its undespread ecological and geographical distributions. Nevertheless, one of the difficulties lies in the incomplete description of many species, and the non-existence of type specimens. The lack of accuracy of descriptions is due, usually, to age of the specimens, and the small number of specimens described, but it is also necessary to point out the difficulties inherent to the morphological criteria used for these descriptions. Our major objectives are to present the various problems remaining within the sub-family Travisiinae, to present the state of the knowledge on this sub-family with a preliminary key, to discuss the generally admitted viewpoints, and to propose a certain number of interpretations and hypothesis as a basis for future work.

## TAXONOMIC STATUS OF GENERA AND SPECIES OF TRAVISIINAE

The sub-family Travisiinae may be defined as following:
Opheliidae with short and grublike body, without lateral and ventral grooves or with very reduced grooves. Branchiae generally present, posterior setigers generally with epipodial pads. Anal cylinder usually short, sometimes furrowed, anal cirri short, and thick setae smooth or finely spinose.

The genus *Travisia* was first described by JOHNSTON (1840) as:

**Diagnosis:** Body short, fusiform or grublike, without distinct groove. Prostomium small, cone-shaped, two nuchal organs. Branchiae present, lateral eyes absent; posterior epipodial pads more or less developed. Parapodial small, without presetal lobes. Lateral sense organs present between parapodial rami. Anal cirri usually short and thick. Setae simple, capillary, or hispid. First setiger appears before the mouth.

Two other genera have been described: *Dindymene* Kinberg, 1866, and *Kesun* Chamberlin 1919.

**Diagnosis**: *Dindymene* Kinberg, 1866 " Corpus fusiforme, segmenta 3-2 annulata, lobus cephalicus minutus, terminalis, nudus; segmenta buccalia tria, primum nudum; os inferum, transversum; pharynx sine papillis et maxillis; pedes duplices, distantes, setis capillaribus: aliis laevibus, aliis serrulato-ciliatis; branchiae cirrosae, usque a segmento buccali secundo; segmenta posteriora tuberculis binis utrinque praedita".

CHAMBERLIN (1919) renamed this genus *Dindymenides* since the original name has been used in 1847 for a Crustacean. He does not give more details on the diagnosis of the genus.

BELLAN *et al.* (1990), following FAUCHALD (1977), kept *Dindymenides* as a valid genus on the basis of a strong autoapomorphy: the serratulate-ciliate setae. However, these authors pointed out that these characters needed to be confirmed. A certain number of Travisiinae belonging to genus *Kesun* and *Travisia* have been also described with hispid and/or serratulated setae. HARTMAN (1948), who examined the Kinberg's material, did not mention these ornamentations. If we consider the position of the first setae with regard to the mouth, HARTMAN stated that the prostomium of the preserved specimen had been unnaturally flattened in a vial, resulting in the misinterpretation of the anterior part of the animal. HARTMAN stated: "the first setae are in front of the oral aperture". Considering the wide variations of the body of the Travisiinae due to their conservation, we accept the opinion of HARTMAN at least until we are in position to examine freshly material. *Dindymene* and thus also *Dindymenides* is known only from a single record (DAY, 1967). In summary, we prefer to consider this genus

Source : MNHN, Paris

invalid, following the opinion of HARTMAN (1948), and more recently FAUCHALD (*in litt.*). The only species known in the genus, originally described as *Dindymene concinna*, must now be known as *Travisia concinna* (KINBERG, 1866).

**Diagnosis**: *Kesun* Chamberlin, 1919. "Body short, pointed at both ends, fusiform or grub-like. Body rounded cylindrically, without ventral groove. Somites of the middle region triannulate, the others may be only biannulate or entire. Prostomium small, wholly smooth and rounded, without processes. Parapodial tubercles small and smooth, or wholly absent. No cirri or branchia on any somite. No eyes. With a series of lateral sensory pits as in *Travisia*. Pygidium small, cylindrical, longitudinally furrowed. Segments not numerous (twenty-eight in the type)".

*Kesun* was created by CHAMBERLIN(1919) for a species *Kesun fusus* distinguishable from the other species of *Travisia* described at that time, by the lack of "cirri" which are commonly interpreted as branchiae. Another feature is the absence of epipodial pads on the last segments and the presence of an anal cylinder. Accepting for the moment the absence of branchiae as a characteristic feature of the genus *Kesun*, we have to point out that other features mentioned, such as the anal cylinder and the lack of epipodial pads in the last setigers are not unique to abrianchiate members of the sub-family. The anal cylinder of *K. fusus* is very short and not really distinguishable from that of *Travisia profundi* and from many other species of the genus. The absence of epipodial pads is also not a unique feature either. This leaves only one unequivoqual difference between *Travisia* and *Kesun*: the absence of branchiae in the latter. In a previous paper, BELLAN *et al.* (1990) argued that this character should not be used at a generic level. The fact that members of *Kesun* are limited to bathyo-abyssal depths might be used as a characteristic feature; however this present time, we propose to discard *Kesun* and retain only a single genus, *Travisia*. HARTMAN (1965a) had already proposed this synonymy. The definition of the genus corresponding to that of the sub-family Travisiinae with a supplementary character: the presence of pustulae or similar structure on the body.

The fact that remains only one genus *Travisia* in the Travisiinae should not change the status of this sub-family. In BELLAN *et al.* (1990), the classification of the Opheliidae family was made using sequencing which means that the first taxa (Travisiinae) is the sister group of all following groups with a rooted tree by a theoric ancestor (see WILLEY, 1981). This classification taking into account the level of apparition in the cladogram was:

Family Opheliidae
- Sub-family Travisiinae
- Sub-family Opheliinae
- Sub-family Ophelininae

This classification regards the very strong differenciation between the Travisiinae and the group Opheliinae + Ophelininae, and respect the classical use of the three sub-families. In the present state of the knowledge, it is not possible to state on the filiation between the Opheliinae and Ophelininae.

## ANALYSES OF TRAVISIINAE SPECIES

We have observed available types or specimens from 21 taxa. The examined specimens come from: 1) Natural History Museum, London, 2) Smithsonian Institution, Washington, 3) Muséum National d'Histoire Naturelle and 4) National History Museum of Los Angeles County. The numbers at the end of these 21 species refer to the museum where they are deposited. A lack of a number indicates that we did not see the specimen. Twenty-seven species and three sub-species are now retained. The alphabetical list of these taxa with indication of the most complete description available, the list of authors having cited the species, and their known geographical distribution is given below:

• *T. antarctica* Hartman, 1967, pp. 139-140; HARTMAN, 1978. South Georgia, Antarctic, South Atlantic Ocean; 2,452-2,727 m. (2)

• *T. arborifera* Fauvel, 1932, pp. 191-193, fig. 33; FAUVEL, 1953. Andaman sea, Gulf of Bengal; British Natural History Museum Collection, 1 ex. off Burma coast, 35 m. Indian Ocean. 7-100 m. (1)

• *T. brevis* Moore, 1923, pp. 220-221; BERKELEY & BERKELEY, 1952, pp. 90-91, fig. 183; BANSE & HOBSON,1968; HARTMAN, 1969, pp. 343-344, 1 fig. BERKELEY & BERKELEY, 1942; IMAJIMA, 1961, 1963, 1964; REISH, 1965; HARTMAN, 1961, 1965b, 1969; FAUCHALD, 1972; LOI, 1980 ; HOBSON, & BANSE, 1981; FAUCHALD & HANCOCK, 1981. Southern California, North-eastern Pacific, Bering Sea, Okhotsk Sea. 18-2,900 m. (2)

• *T. carnea* Verrill, 1873, pp. 508 & 604; EHLERS, 1887; PETTIBONE, 1954, pp. 296-298; APPY *et al.*, 1980. According to HOBSON & BANSE, 1981, the designation of *T. carnea* by BERKELEY, 1966, 1968 for British

Source : MNHN, Paris

Columbia is incorrect; it is probably *T. pupa*. We have seen the holotype of *T. parva* Day, 1973 (p. 94, fig. 13), off Beaufort, North Carolina. It has: 20 setigers, a posterior asetigerous segment, 19 pairs of branchiae, neither parapodial lappets nor lateral crenulations. These characters are very similar of those of *T. carnea* Verrill, 1873, and it is surprising that DAY didn't compare his species with the Verrill's species which are found in the same area and depth. We consider *T. parva* as a synonym of *T. carnea*. North-western Atlantic, Massachussets to long Island, Arctic Alaska. 5-35 m. (2)

• *T. chiloensis* Kükenthal, 1887, pp. 364-365, figs 1-3. Chiloe, South-eastern Pacific.

• *T. chinensis* Grube, 1869, p. 66; AUGENER, 1922, pp. 38-40. China Sea, North-western Pacific.

• *T. concinna* (Kinberg, 1866), p. 256; KINBERG, 1910, p. 66, plate 25, fig. 5; HARTMAN, 1948, pp. 113-114. Algoa Bay, South Africa, 5-20 m.

• *T. doellojuradoi* Rioja, 1944, pp. 135-136, figs 57-59; RIOJA, 1946. Argentina coasts, South-western Atlantic. 115 m.

• *T. elongata* Grube, 1866, p. 66; EHLERS, 1901, p. 171, plate 22, figs 11-14. AUGENER, 1922, p. 34. Iquique, Perou, South-eastern Pacific.

• *T. foetida* Hartman, 1969, pp. 344-345, three figures; FAUCHALD, 1972, pp. 237-238, plate 49, fig. d; FAUCHALD & HANCOCK, 1981; MOORE, 1923, HARTMAN, 1963, 1965b, 1966a as *T. pupa*. Redondo Canyon, California, North-eastern Pacific. 250-3,100 m. (4)

• *T. forbesii* Johnston, 1840, pp. 373-374, plate 19, figs 11-18; RATHKE, 1843, pp. 192-194, plate 10, figs 9-12. de SAINT JOSEPH, 1898; McINTOSH, 1908a, b; FAUVEL, 1914, 1925; ANNEKOVA, 1937, 1938; BERKELEY & BERKELEY, 1942; STÖP-BOWITZ, 1945, 1948; WESENBERG-LUND, 1950, 1951; PETTIBONE, 1956; CHLEBOVITSCH, 1961; DAY, 1961, 1967; ELIASON, 1962; HARTMAN, 1965a; HAMOND, 1966; CABIOCH *et al.*, 1968; RETIÈRE, 1968; GLÉMAREC, 1969; KIRKEGAARD, 1969; AMOUREUX, 1971; LEVENSTEIN, 1966, 1971/72; WOLFF, 1973; AVERINCEV, 1977; HOLTHE, 1977; HOBSON, & BANSE, 1981. According to STÖP-BOWITZ (1948) and as EHLERS (1897), the designation of *T. forbesii* from the coasts of Chile and Antarctic is doubtful. *T. forbesii* is characteristic of the northern hemisphere where it is collected to 300 m (LEVENSTEIN, 1971/72). One specimen of *T. forbesi* with 28 setigers from False Bay, South Africa, is in the collection of the Natural History Museum of London. We confirm the presence of the species in South Africa. Arctic, Circumpolar: Novaya Zemlya, Davis Strait, Spitsbergen, Kara sea, Alaska and Canadian Arctic, North-east America, Siberia, Bering sea to Washington Sound, North Japan Sea, West and east Greenland, Iceland, Faroes, Norway, North sea, western Baltic, Great Britain, France; off the mouth of the Amazone, Brazil, South Africa. 0-3,000 m. (1, 3)

• *T. forbesii intermedia* (Annenkova, 1937), p. 177; USCHAKOV, 1955; BUZHINSKAYA, 1985. According to BUZHINSKAYA (1985), we have considered *T. kerguelensis* McIntosh subsp. *intermedia* Annekova, 1937 as a *T. forbesi* subsp. *intermedia* (Annekova, 1937). Japon Sea, North-western Pacific. 30 m to abyssal.

• *T. fusiformis* Kudenov, 1975, pp. 215-218, figs 17-23. Gulf of California, Mexico, North-eastern Pacific. Intertidal. (4)

• *T. fusus* (Chamberlin, 1919), p. 386, plate 67, fig. 5 and plate 68, figs 1-2; LEVENSTEIN, 1970, 1971/72. Pacific Ocean. 3,000-7,580 m. (2)

• *T. gigas* Hartman, 1938, p. 103, figs 46-48; HARTMAN, 1961, 1963; BERKELEY & BERKELEY, 1941, 1962; BERKELEY, 1968; REISH, 1968; HOBSON & BANSE, 1981. California, North-eastern Pacific. 0-180 m. (2)

• *T. glandulosa* McIntosh, 1879, p. 506, figs. 15-16. We have seen the only known specimen of *T. glandulosa*. It was found in North-western Atlantic at 3,300 m. It has: 7 mm length, no visible branchiae, a very distinct lateral groove at the last setigers, pustulae in a row by annulus. These characters are very similar to those of *Kesun abyssorum* Monro, 1930. Even if *T. glandulosa* was rather poorly described by McINTOSH, it does not seem that Monro compare his specimen with McINTOSH's species. Considering the similarity of *Kesun abyssorum* Monro, 1930 with *Travisia glandulosa* McIntosh, 1879, we propose the synonymy of the two species. MONRO, 1930, p. 167, fig. 69 8 8; KIRKEGAARD, 1956, p.71, fig.10; HARTMAN, 1966b, p. 51; MONRO, 1939; AUGENER, 1932; HARTMAN, 1967; LEVENSTEIN, 1961a, 1961c, 1971/72, 1975, 1978; AVERINCEV, 1974; ROZBACZYLO, 1985. Pacific Ocean, Antarctic Ocean, Atlantic Ocean. 193-6,850 m. (1)

• *T. granulata* Moore, 1923. pp. 219-220; HARTMAN, 1938, 1961, 1969; LOI, 1980. Southern California, North-eastern Pacific. 45-105 m. (2)

• *T. gravieri* (McINTOSH, 1908a), pp. 383-384; McINTOSH, 1915, pp 29-30, plate 95, fig. 8; HARTMAN, 1965a, pp. 191-192; HARTMAN & FAUCHALD, 1971; LEVENSTEIN, 1971/72; AMOUREUX, 1982; KIRKEGAARD, 1980. Atlantic Ocean. 539-7,800 m. (1)

• *T. hobsonae* Santos, 1977, pp. 559-564, fig. 1; UEBELACKER, 1984, pp. 17-4, 17-5, figs 17-1, 17-2. Gulf of Mexico, North-western Atlantic. 10-110 m. (2)

Source : MNHN, Paris

• *T. horsti* Caullery, 1944, pp. 47-48, fig. 40. Java Sea, Pacific. 959 m.
• *T. japonica* Fujiwara, 1933, pp. 91-103, plate I, figs 1-8, plate II, figs. 1-6; MONRO, 1934, pp. 373-374, fig. 8 as *T. chinensis* Grube, 1869 according to HARTMAN, 1959; FAUVEL, 1936, pp. 75-78. FAUVEL, 1933; USCHAKOV, 1955; IMAJIMA & HARTMAN, 1964, BERKELEY, 1966; UCHIDA, 1967; HOBSON & BANSE, 1981; FOURNIER & LEVINGS, 1982; BUZHINSKAYA, 1985. Japan Sea, North-western Pacific. 10-105 m. (1, 3)
• *T. kerguelensis* McIntosh, 1885, pp. 357-359, plate 43, fig. 10, plate 36A, figs 1-2; EHLERS, 1897, pp. 97-98, plate 6, figs. 159-161; AUGENER, 1922, pp. 36-37; HARTMAN, 1966b, p. 54, plate 17, figs 4-5; AVERINCEV, 1982, p. 34, plate 5, figs 12-14; EHLERS, 1901, 1908, 1912; AUGENER, 1923, 1932; MONRO, 1930, 1936, 1939; FAUVEL, 1941; RIOJA, 1944, 1946; HARTMAN 1953, 1967, 1978; KNOX, 1962; AVERINCEV, 1974; DAY & HUTCHINGS, 1979; ROZBACZYLO, 1985; HARTMANN-SCHRÖDER, 1986; HARTMANN-SCHRÖDER & ROSENFELDT, 1989. Kerguelen, Southern Indian, Southern Atlantic, Antarctic Ocean. 0-1,837 m. (1, 3)
• *T. kerguelensis gravieri* Monro, 1930, p. 167, fig. 68; HARTMAN, 1966b; HARTMANN-SCHRÖDER & ROSENFELDT, 1989. Palmer Archipelo, Antarctic Ocean. 259-315 m. (1)
• *T. lithophila* Kinberg, 1866, p. 256; AUGENER, 1922, pp. 32-33; HARTMAN, 1966b, p. 54, plate 17, figs 7-10. HUTCHINGS & MURRAY, 1984, p. 79; HARTMAN, 1952. Australia, South-western Pacific. 20-180 m.
• *T. nigrocincta* (Ehlers, 1913), p. 525; HARTMAN, 1966b, 1967. South Pacific, Antarctic. 2,725 m.
• *T. olens* Ehlers, 1897, p. 98-99, plate 6, figs 162-163; AUGENER, 1922, pp. 35-36; EHLERS, 1901, 1912; MONRO, 1930; AUGENER, 1932; BENHAM, 1950; HARTMAN, 1966b, 1967; DAY & HUTCHINGS, 1979. HARTMANN-SCHRÖDER & HARTMANN, 1980; ROZBACZYLO, 1985. One ex. Discovery st 939, 08/18/1932, 35°49'6S-173°27'E, 87 m. The designation of *T. olens* by FAUVEL, 1943 from California was probably incorrect, HARTMAN, 1969 did not cite the species from California. It may be *T. granulata*. Cape Horn, Scotia Sea, South-western Atlantic, Antarctic, New Zealand, South-eastern Pacific. 0-1,120 m. (i)
• *T. olens* Ehlers *novae zealandiae* Benham, 1927, pp. 123-128, plate 2, figs 70-72. EHLERS, 1897, 1907, 1912 as *T. olens*; BENHAM, 1950, DAY & HUTCHINGS, 1979. British Natural History Museum Collection: 9 ex. from Portobello. South Island, New Zealand. New Zealand, South-western Pacific. 0-20 m. (1)
• *T. oregonensis* Fauchald & Hancock, 1981, p. 19. Offshore Oregon, North-eastern Pacific. 1,600-1,800 m. (4)
• *T. profundi* Chamberlin, 1919, pp. 387-389, plate 67, figs 1-4; USCHAKOV, 1955; KIRKEGAARD, 1956; LEVENSTEIN, 1960, 1961a, b, 1966, 1970, 1971/72, 1975, 1978; HARTMAN, 1967. Atlantic (Angola) and Pacific Ocean (Mid Bassin), Antarctic Ocean. 975-7,290 m. (2)
• *T. pupa* Moore, 1906, pp. 228-230, plate 11, fig. 29; TREADWELL, 1914; USCHAKOV, 1955; LEVENSTEIN, 1960, 1961b, 1966, 1971/72; HARTMAN, 1961; BERKELEY, 1966, 1968; BERKELEY & BERKELEY, 1942, 1952; HOBSON & BANSE, 1981. North eastern Pacific. 33-3,012 m. (2)

## DISCUSSION OF THE MORPHOLOGICAL CHARACTERS

The shared characters of all species of *Travisia* include the presence of nuchal organs and interramal sense organs; the capillary setae are often hispid and all species lack eyes. Characters used to distinguish the species include the presence of lobes or papillae on the pygidium, the position of the nephridiophores and the total number of setigers present. Few characters are unique to a single taxon. The body-shape is more variable, more or less fusiform or grub-shaped, but the shape may vary with the numbers of segments present and with the quality of fixation. The prostomium is pointed in all species, except in *T. foetida*, which is truncate. Lateral and mid-ventral grooves are generally absent; the development of these grooves characterize the different sub-families, however they are present, but poorly developed in some taxa. For example, a short lateral groove is present in *T. glandulosa* and a mid-ventral one in *T. fusiformis*, *T. gravieri* and *T. hobsonae*. Branchiae are present except in the species being transferred from *Kesun: T. fusus, T. glandulosa, T. gravieri*, and *T. nigrocincta*. The branchiae are cirriform except in *T. arborifera* which has branching branchiae. They are present from setiger 2, except in *T. hobsonae*, sometimes in *T. carnea*, and *T. profundi* where they are present from setiger 3. Unusual lobes or papillae are present on the pygidium in *T. japonica, T. gigas, T. kerguenlensis gravieri*. Nephridiopores are present on setigers 3-14 except in *T. brevis* (7-25), *T. chiloensis (7-14?), T. japonica* (11-14 in the original description but 3-14 in Fauvel, 1933). The number (n) of setigers is relatively stable in a given species (n ± 5) except in *T. granulata* 32-50, *T. japonica* 32-39 and *T. lithophila* 44-53. It would be interesting to study the actual significance of this variability as a possible character at the specific level.

A last point, is the variability of the degree of papillation in the posterior segments as described in *T. kerguelensis* by MONRO (1930). Some difficulties remain in ascertaining the identity of four similar taxa, all

Source : MNHN, Paris

described from southern oceans. They were distinguished on the number of segments and the papillation: *T. kerguelensis* (23-27 segments), T. *kerguelensis gravieri* (25), *T. olens* (29-36), and *T. olens novae zealandiae* (38-40).

## PRELIMINARY KEY TO THE TRAVISIINAE

A preliminary key of the species *Travisia* is presented which is provisional due to the difficulties in correctly interpreting the available descriptions, some of which are incomplete. The need of a phenetic and phylogenetic study is necessary in order to test the validity of characters. Before, this can be done, it is necessary to have a complete redescription for all species. The following characters must be accurately described in all species:

- color and shape of live specimen;
- presence, shape, and variability of posterior lateral crenulations and parapodial lappets;
- number and variability of number of segments and setigers;
- number of branchiae;
- distribution of pustulae on the body;
- shape of the pygidium and pygidial papillae.

**1** Branchiae absent ..... **2**
Branchiae present ..... **5**

**2** Lateral groove in the last 10 segments..... *T. glandulosa*
Lateral groove absent ..... **3**

**3** Body grub-shaped, < 25 segments, mid-ventral groove present, very short setae ..... *T. gravieri*
Body fusiform, ≥ 25 segments, fascicles of distinguished setae ..... **4**

**4** Segment number 28, ≥ 25 setigers ..... *T. fusus*
Segment number 25, 17 setigers..... *T. nigrocincta*

**5** Prostomium truncated, 31 setigers, large species..... *T. foetida*
Prostomium pointed conical ..... **6**

**6** Branchiae branched ..... *T. arborifera*
Branchiae cirriform ..... **7**

**7** Mid-ventral groove present ..... **8**
Mid-ventral groove absent ..... **9**

**8** Mid-ventral groove slightly developed, 30-31 setigers, parapodial lappets developed ..*T. hobsonae*
Mid-ventral groove and parapodial lappets well developed, 34-35 setigers..... *T. fusiformis*

**9** Segment number > 40..... **10**
Segment number ≤40..... **13**

**10** Posterior parapodia with lobes or lappets ..... **11**
Posterior parapodia without lobes or lappets ..... **12**

**11** Posterior parapodia with triangular lappets, pygidium collarlike with 6 long dorsal papillae, length about 10 cm..... *T. gigas*
Posterior parapodia with small lappets, knob pygidium, length about 3 cm ..... *T. elongata*

**12** Epithelium with large, dorsal and ventral coarse pustules, setiger number to about 45, pygidium with 12-13 irregular papillae..... *T. granulata*
Epithelium finely reticulated, from 44 to 53 setigers, pygidium with 7 cirri ..... *T. lithophila*

**13** Segment number > 30 ..... **14**
Segment number ≤ 30 ..... **18**

**14** Posterior lappets absent, 26-45 setigers ..... *T. granulata*

Source : MNHN, Paris

Posterior lappets and lateral crenulations developed ..... **15**

**15** Pygidium with an oval ventral lobe and 6 laterodorsal palpi ..... **16**
Pygidium shape otherwise ..... **17**

**16** Laterodorsal palpi well developed, segment number 32-39, 26-32 branchiae pairs ..... *T. japonica*
Segment number 35, 33 pairs of branchiae ..... *T. concinna*

**17** Segment number 29-32 ..... *T. olens*
Segment number 38-40 ..... *T. olens novae zealandia*

**18** Setigers number = 18, 23 segments ..... *T. orogenensis*
Setigers number ≥ 20 ..... **19**

**19** Parapodial lappets reduced or absent ..... **20**
Parapodial lappets present ..... **23**

**20** Setigers number ≥ 20, 25-29 segments, pygidium small, longitudinally furrowed ..... *T. carnea*
Setigers number ≥ 25 ..... **21**

**21** Numbers of branchiae pairs 9-12, 26 setigers and 25-27 segments ..... *T. profundi*
Numbers of branchiae ≥ 15 ..... **22**

**22** Segments number 30-32, 25-28 setigers, 22-25 pairs of branchiae number ..... *T. pupa*
Segments number < 30, about 25 setigers, 17-21 pairs of branchiae, anal cylinder surrounded by a circlet of short papillae ..... *T. antarctica*

**23** Body pigmented in red purple, 17 pairs of branchiae ..... *T. doellojuradoi*
Body not pigmented in red purple, ≥ 18 pairs of branchiae ..... **24**

**24** 2 posterior achaetous segments ..... **25**
3-5 posterior achaetous segments ..... **28**

**25** Parapodial lappets well developed, posterior part of the body finishing truncated ..... **26**
Parapodial lappets little developed, posterior part of the body tapered to the pygidium ..... **27**

**26** Lateral lappets well developed, pygidium cylindrical ..... *T. kerguelensis*
Laterals lappets absent, a pair of dorsal anal cirri at the end of the anal cylinder ..... *T. kerguelensis gravieri*

**27** Setigers number 23-26, posterior margin of abdominal segment smooth, not scalloped, pygidium ovoid ..... *T. forbesii*
Setigers number 26-29, posterior margin of abdominal ondulate or serrulate, pygidium cylindrical ..... *T. forbesii intermedia*

**28** Parapodial lappets little developed, pygidial knob pigmented, 23 setigers, 28 segments ..... *T. horsti*
Parapodial lappets developed, pygidium not pigmented ..... **29**

**29** Branchiae number ≥ 20, 27 segments, 24 setigers ..... *T. chiloensis*
Branchiae number ≤ 20, 29 segments ..... **30**

**30** Setigers number 23-25 ..... *T. brevis*
Setigers number 27 ..... *T. chinensis*

## BIOGEOGRAPHICAL DISTRIBUTION

Table 1 summarizes available data of species distribution. Only two species occur in Arctic Ocean; Antarctic Ocean is richer with eight taxa. *T. antarctica* is present in the far-south (South Georgia) of the Atlantic Ocean. Ten species are present in the Atlantic Ocean, two of which are restricted to the northern part, five to the southern part

Source : MNHN, Paris

and three have an extended distribution. Twenty-one taxa are present in the Pacific Ocean, 13 are restricted to the north, with *T. arborifera* found in the Gulf of Bengal which is the single species collected in the Indian Ocean. Six species are known to be only from the south Pacific Ocean. Eight species have a large biogeographical distribution: *T. glandulosa, T. forbesi, T. fusus, T. gravieri, T. japonica, T. kerguelensis, T. olens,* and *T. profundi.*

TABLE 1. — Biogeographical distribution of *Travisia* species from the world's oceans.

| | Arctic | Atlantic | Patagonian | Pacific | Antarctic |
|---|---|---|---|---|---|
| Shelf | *brevis forbesii* | | | | *kerguelensis, olens, lithophila* |
| Boreal NE | | *forbesii* | | *brevis, forbesii, gigas, japonica, pupa* | |
| Boreal NW | | *carnea, forbesii* | | *brevis, forbesii, japonica* | |
| Lusitanic | | *forbesii* | | | |
| W. Tropical and Indian | | | | *arborifera, chinensis, japonica* | |
| Carribean | | *hobsonae* | | *fusiformis, gigas, granulata* | |
| S. America tropical | | *forbesii doellojuradoi* | | | |
| S. Africa tropical | | *concinna forbesii* | | | |
| Tasmania N.Z. | | | | *kerguelensis, lithophila, olens, olens n.z.* | |
| Araucanic | | | *chiloensis kerguelensis, olens, olens n.z.* | *elongata* | |
| Bathyal Abyssal | *forbesii* | | | | *glandulosa, antarctica kerguelensis, k. gravieri, nigrocincta, olens, profundi,* |
| North | | *glandulosa, forbesii, gravieri,* | | *glandulosa, forbesii, profundi, pupa* | |
| East | | *glandulosa, gravieri* | | *glandulosa, brevis, foetida, forbesii, fusus, orogonensis profundi, pupa* | |
| West | | *antarctica, forbesii, gravieri* | | *glandulosa f. intermedia fusus, horsti,, olens, profundi, pupa* | |

## BATHYMETRIC DISTRIBUTION

Three species *T. chiloensis, T. chinensis* and *T. elongata* were described without indication of original depth, and were probably littoral species. Among the other 27 taxa, 16 are present in the bathyal and/or the abyssal depths and 10 are exclusively bathyo-abyssal (Fig. 1). Eighteen species are found on the continental shelf among which only five species are collected at depths less than 100 m.

Source : MNHN, Paris

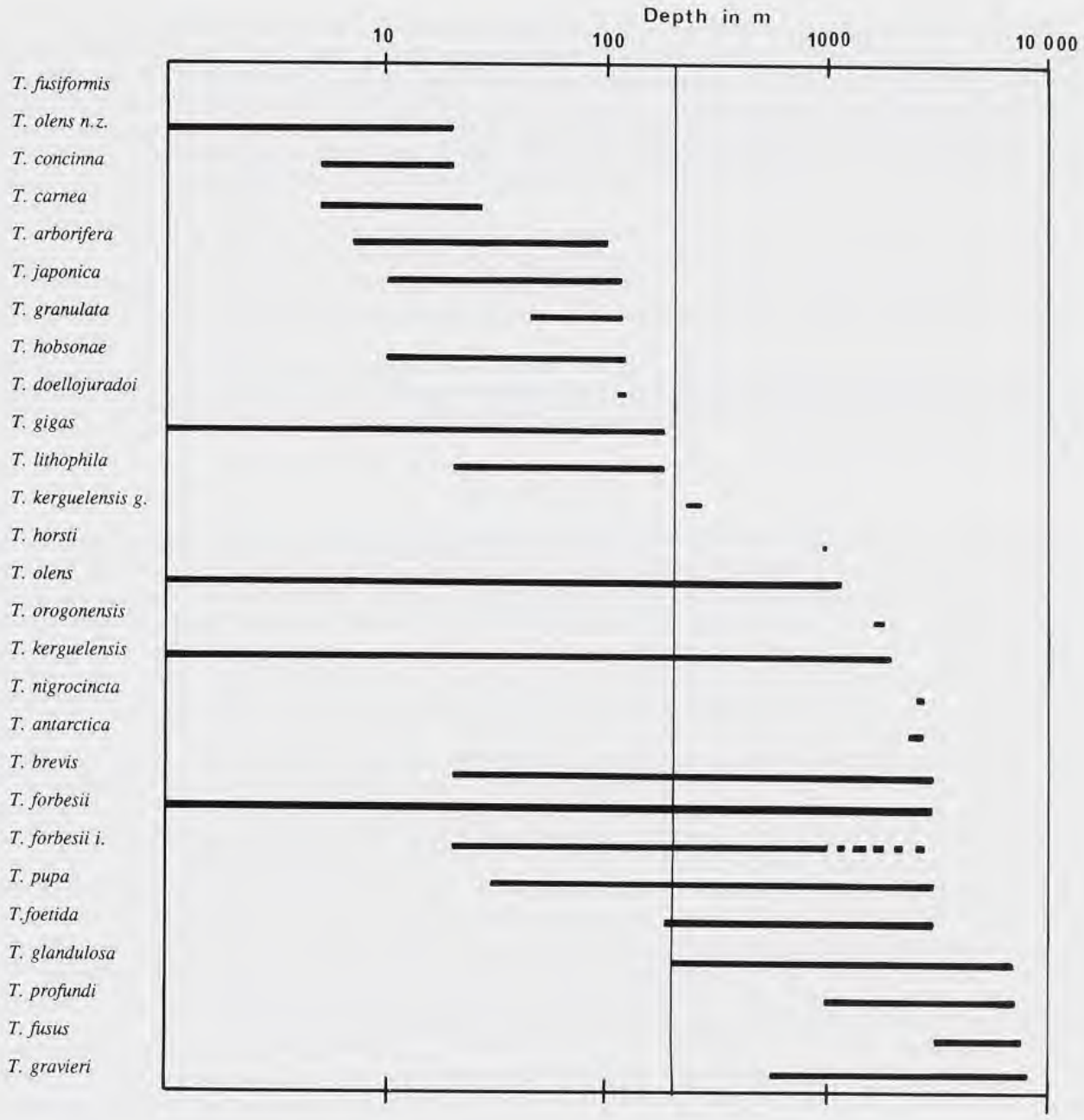



FIG. 1. — Bathymetric distribution of *Travisia* species from the world's oceans.

Source : MNHN, Paris

## ECOLOGICAL AND BIOLOGICAL DISTRIBUTION

The data on the ecology of the species are rarely reported and therefore the ecological and biological data are incomplete. Most of the deeper species are found in bathyal and abyssal mud. The littoral species are found especially in muddy and fine sand. *T. foetida* inhabits essentially clean sands in low intertidal and in the upper part of the subtidal. However, this species has been found also in many different types of soft-bottom substrates. Due to its widespread distribution both geographical and bathymetric, *T. forbesii* appears to be ubiquitous. This ubiquity may be the result of the presence of a complex of species. The principally northern species *T. forbesi* may have a counterpart in the southern hemisphere with *T. kerguelensis* and *T. olens* and their sub-species.

*Travisia* are considered non-selective deposit-feeders. In the intertidal sand at Tampa Bay, Florida, specimens of *Travisia hobsonae* had only sand particles in their gut with no particles finer than 100 µm ; grains as large as 475 µm were removed with a median size of 230 µm (DAUER, 1980). The low level of food specialization in adults contrasts sharply with the high level of precision in the selection of substrata by juveniles (RETIÈRE, 1971, 1972).

*Travisia forbesi* lives 3.5 years at Dinard (English Channel); the spawning occurs at the end of the autumn and during the winter; development is direct without larval dispersion (RETIÈRE, 1971, 1972). *T. hobsonae* reproduces the year round in Tampa Bay (DAUER, 1980); its densities could reach an annual average of 1,100 $m^{-2}$ at certain stations.

## DISCUSSION

This paper is a first step toward the study of Travisiinae and to the knowledge of the Opheliidae family. The sub-family Travisiinae is the most plesiomorph (BELLAN *et al.*, 1990) and is well defined in relation to the two other sub-families. This paper proposes to bring together all the species of this sub-family into the one genus *Travisia* Johnston, 1840. The examination of available types has allowed us to place into synonymy *Kesun abyssorum* Monro, 1930 with *Travisia glandulosa* McIntosh, 1879, and *T. parva* Day, 1973 with *T. carnea* Verrill, 1873. Five species *T. chiloensis, T. chinensis, T. concinna, T. elongata* and *T. horsti* which have not (or rarely) been found since their description, remain doubtful and must be re-examined. Many characters should be used in defining each species: color and shape of live specimens; presence, shape, and variability of posterior lateral crenulations and parapodial lappets; number and variability of number of segments and setigers; number of branchiae; distribution of pustulae on the body; shape of the pygidium and pygidial papillae. The variability of the number of setigers, segments, and branchiae must be defined using a large number of specimens of each species. This work would allowed in a further step to study the phenetic and the phylogenetic relationship between the species. However, genetical studies must be established: 1) the real extended distribution of *T. forbesii* and *T. forbesii intermedia* (northern species) ; *T. forbesii* may be a complex with slight morphological differences; 2) the genetical distance and variability of the southern species and their sub-species: *T. kerguelensis, T. kerguelensis gravieri, T. olens* and *T. olens novae zealandiae*. These four taxa are distinguishable essentially by the number of segments and setigers, so they show a continuum between *T. kerguelensis* with a number of segments which could be reduced to 23 and *T. olens novae zealandiae* which a number of segments reaching 40. *T. kerguelensis* is known to show a great variability of papillation in the posterior segments (MONRO, 1930).

It is clear that the data on ecological and biological features are insufficient. Biological data are limited to *T. forbesii* and *T. hobsonae*. Such studies must be extended to other species and populations. In the past few years several works on *Ophelia*, such as those of RISER (1987) and HARRIS (1991) have demonstrated that biological (type of development) and ecological data (habitat) could be good criteria to ascertain on the validity of a particular species in this family.

*Travisia* is typically a deep water Pacific genus. Bathymetric distributions of *Travisia* and *Ophelia* (BELLAN & DAUVIN, 1991) show that *Ophelia* occurs preferentially in shallow waters and in the Atlantic whereas *Travisia* species dominate in the bathyal and abyssal depths in the Pacific. This indicates that the speciation of these two genera could be parallel. In Ampeliscidae (Amphipoda), another marine diversified family, DAUVIN & BELLAN-SANTINI (1990) have also distinguished two distribution schemes with *Ampelisca* in shallow water and *Haploops* in continental and bathyal depths.

New data are need before elucidating the evolution of the genus. Future works and prospects on *Travisia* genus, but also on other genera of Opheliidae may reveal correlations between species, phyletic, bathymetric and biogeographic features.

Source : MNHN, Paris

## ACKNOWLEDGEMENTS

The authors would like to thank their colleagues for lending types and specimens deposited in the collections, Dr Alex MUIR, Natural History Museum, London, Drs K. FAUCHALD and L. WARD, Smithsonian Institution, Washington, L.H. HARRIS, Natural History Museum of Los Angeles County, Dr FAUCHALD also for his remarks on the Travisiinae. Dr Alex MUIR was particularly hepful during the visit in London of J.C. DAUVIN, which was made possible by a grant from the M.N.H.N. (Bonus Qualité Recherche, Muséum 1991, M31). They also wish to thank P. GILLET for access to the library of the Catholic University of Angers, A.B. DAVIES, Emory Univ., Atlanta, GA, for her help in correcting the manuscript, and D. REISH and K. FAUCHALD for their very constructive suggestions on the first draft.

## REFERENCES

AMOUREUX, L., 1971. — Annélides Polychètes capturés au large de la côte d'Arcachon. Inventaire taxonomique. *Bull. Soc. Linn. Bordeaux*, **1** : 147-164.

AMOUREUX, L., 1982. — Annélides Polychètes recueillies sur la pente continentale de la Bretagne à l'Irlande, campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre nouvelles espèces pour la science. II. Inventaire taxonomique annoté de toutes les Polychètes Sédentaires. *Cah. Biol. mar.*, **23** : 179-214.

ANNEKOVA, N., 1937. — The polychaete fauna of the northern part of the Japan Sea [in russian]. *Issledovaniya Fauny Morei. SSSR.*, **23** : 139-316.

ANNEKOVA, N., 1938. —Polychaeta of the North Japan Sea and their horizontal and vertical distribution. Hydrobiol. Exped. U.S.S.R. in 1934 to the Japanese Sea [in russian]. *Trudy D.-V. Filial Akad. Nauk.*, **1** : 81-230.

APPY, T.D., LINKLETTER, L.E & DADSWELL, M.J., 1980. — A guide to the Marine Flora and Fauna of the bay of Fundy : Annelida: Polychaeta. *Fish. & Mar. Service Tech. Rep.*, **920** : 1-124.

AUGENER, H., 1922. — Revision der australischen Polychaeten-Typen von Kinberg. *Arkiv für Zool.*, **14** : 1-42.

AUGENER, H., 1923. — Polychaeten von den Auckland und Campbell-Inseln. *Vidensk. Medd. naturh. Foren. Köbenhavn*, **75** : 1-115.

AUGENER, H., 1932. — *Antarktische und Antiboreale polychaeten nebst einer Hirudinae*. Scientific Results of the Norwegian Antarctic Expedition 1927-28. Norske Videnskaps Akad. Oslo, 86 pp.

AVERINCEV, V.G., 1974. — The polychaetous annelids of the abyssal and bathyal zones of the Scotian arc based on the 11 th cruise of R/V "Akademik Kurchatov" [ in russian]. *Trudy Inst. Okeanol. Moscou*, **98** : 213-227.

AVERINCEV, V.G., 1977. — Explorations of the fauna of the seas. Biocoenoses of the shelf of franz Josef Land and the fauna of adjacents waters [in russian]. *Acad. Sci. U.S.S.R.*, **14** : 140-184.

AVERINCEV, V.G., 1982. — Seasonal variations in the sublittoral polychaetes fauna (Polychaeta) of the Davis Sea [in russian]. *Issledovaniya Fauny Morei, SSSR*, **28** : 4-70.

BANSE, K. & HOBSON, K.B., 1968. — Benthic polychaetes from Puget Sound, Washington, with remarks on four others species. *Proc. U.S. Nat. Hist. Mus.* **125**, 3667: 1-53.

BELLAN, G., BELLAN-SANTINI , D. & DAUVIN, J.C., 1990. — Phénétique et phylogénie des Opheliidae (Annélides Polychètes). *C. R. Acad. Sci. Paris*, **310**, sér. III : 175-181.

BELLAN, G. & DAUVIN, J.C., 1991. — Phenetic and biogeographic relationships in *Ophelia* (Polychaeta, Opheliidea). *Bull. Mar. Sci.*, **48** : 544-558.

BELLAN-SANTINI, D., DAUVIN, J.C. & BELLAN, G. , 1992. — Approche phénétique et phylogénétique des *Ophelia* (Annélides Polychètes) de Méditerranée occidentale. *Bull. Inst. Océanogr. Monaco*, n° spéc. **9** : 67-81.

BENHAM, W.B., 1927. — Polychaeta. British Antarctic Terra Nova Expedition 1910. *Nat. Hist. Rep., Zoology*, **7** : 47-182.

BENHAM, W.B., 1950. — Polychaeta of the Auckland and Campbell Islands. *Bull. Cap. Exped. Ser. Wellington N. Z.*, **10** : 1-26.

BERKELEY, C., 1966. — Records of some species of Polychaeta new to British Columbia and of extension in distribution of some others. *Can. J. Zool.*, **44** : 839-849.

BERKELEY, C., 1968. — A checklist of Polychaeta recorded from the British Columbia since 1923, with references to name changes descriptions, and synonymies II. Sedentaria. *Can. J. Zool.*, **46**: 557-567.

Source : MNHN, Paris

BERKELEY, E. & BERKELEY, C., 1941. — On a collection of Polychaeta from southern California. *Bull. S. California Acad. Sci.*, **40** : 16-80.

BERKELEY, E. & BERKELEY, C., 1942. — North Pacific Polychaeta from the west coast of Vancouver Island, Alaska and Bering Sea. *Can. Jour. Res. Ottawa*, **20** : 183-208.

BERKELEY, E. & BERKELEY, C., 1952. — 9. Annelida, Polychaeta Sedentaria. *Canadian Pacific Fauna, Fish Res. Bd Canada*, **9b** : 1-139.

BERKELEY, E. & BERKELEY, C., 1962. — Polychaeta from the British Columbia with a note on some Western Canadian artic forms. *Can. J. Zool.*, **40** : 571-577.

BUZHINSKAYA, G.N., 1985. — Polychaeta of the shelf off south Sakhalin and their ecology [in russian]. *Issledovaniya Fauny Morei, SSSR*, **30** : 72-224.

CABIOCH, L., L'HARDY, J.P. & RULLIER, F., 1968. — Inventaire de la faune marine de Roscoff. Annélides. *Trav. Stat. Biol. Roscoff*, **17** : 1-95.

CHAMBERLIN, R.V., 1919. — The Annelida Polychaeta. *Mem. Mus. Comp. Zool. Harvard.*, **48** : 1-514.

CAULLERY, M., 1944. — Polychètes sédentaires de l'expédition du Siboga : Ariciidae, Spionidae, Chaetopteridae, Chloraemidae, Opheliidae, Oweniidae, Sabellariidae, Sternaspidae, Amphictenidae, Ampharetidae, Terebellidae. *Siboga Exped.*, **24** : 1-204.

CHLEBOVITSCH, V.V., 1961. — Polychètes littorales des Kouriles [in russian]. *Rech. Mers Lointaines de L'Ouest de l'U.R.S.S.*, **7** : 151-260.

DAUER, D.M., 1980. — Population dynamics of the polychaetous Annelids of an intertidal habitat in the upper old Tampa Bay, Florida. *Int. revue ges. Hydrobiol.*, **65** 461-487.

DAUVIN, J.C. & BELLAN-SANTINI, D., 1990. — An overview of the Amphipod genus *Haploops* (Ampeliscidae). *J. mar. biol. Ass. U.K.*, **70** : 887- 903.

DAY, J.H., 1961. — The polychaete fauna of South Africa. Part 6. *J. Linn. Soc. London*, **4**, 469-560.

DAY, J.H., 1967. — *A monograph on the Polychaeta of Southern Africa. Part II. Sedentaria.* British Museum Natural History Publication, London, 878 pp.

DAY, J.H., 1973. — New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *NOAA Tech. Rep. NMFS*, **375** : 1-140.

DAY, J.D. & HUTCHINGS, P., 1979. — An annotated checklist of Australian and New Zealand polychaeta, Archiannelida and Myzostomida. *Rec. Austr. Mus.*, **32** : 80-161.

EHLERS, E., 1887. — Report on the annelids of the dredging expedition of the U.S. coast survey Steamer Blake. *Mem. Mus. Comp. Zool.*, **15** : 1-335.

EHLERS, E., 1897. — *Polychaeten.* Hamburger Magellhaenische Sammelreise, Hamburg, 148 pp.

EHLERS, E., 1901. — *Die Polychaëten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch.* Festschrift zur Feier des Hunderfünfzijähringen Bestehens des königlichen Gesellschaft der Wissenschaften zu Göttingen (Abh. Math.- Phys.). Berlin, 232 pp.

EHLERS, E., 1907.— Neusselandische Anneliden. II. *K. Ges. wiss. Göttingen, Math-Phys. Kl., Abh., n. Folge*, **5** : 1-31.

EHLERS, E., 1908. — *Wissenschaftliche Ergebnisse der deutschen Tiefsee-expedition auf dem Dampfer Valdivia 1898-1899. Im Auftrage des Reichsamtes des Innern, herausgegeben von Carl Chun, Professor der zoologie in Leipzig, Leiter der Expedition, 16, 1. Die Bodensässigen Anneliden aus den Sammlungen der deutschen Tiefsee-Expedition.* Jena, Gustav Fischer, 168 pp.

EHLERS, E., 1912. — Polychaeta. National Antarctic Expedition, 1901-1904. *Nat. Hist., 6 (Zool.)* : 1-32.

EHLERS, E., 1913. — Die Polychaëten Sammlungen des deutschen Südpolar Expedition 1901-1903. *Deutsche Südpolar Exped.*, **13** : 397-598.

ELIASON, A., 1962. — Undersöknigar över Öresund. 41. Weitere Untersuchungen über die Polychaeten -fauna des Öresunds. *Acta. Univ. Lun.*, **2**, 16 : 1-103.

FAUCHALD, K., 1972. — Benthic Polychaetous annelids from the deep water off western Mexico and adjacent areas in the eastern pacific ocean. *Allan Hancock Monogr. Mar. Biol.*, **7** : 1-575.

Source : MNHN, Paris

FAUCHALD, K., 1977. — The polychaete worms. Definitions and keys to the Orders, Families and genera. *Nat. Hist. Mus. Los Angeles county, Sci., ser.* **28** : 1-190.

FAUCHALD, K. & HANCOCK, D.R., 1981. — Deep-water Polychaeta from a transect off central Oregon. *Monogr. Ser. Allan Hancock Found.*, **11** : 1-73.

FAUVEL, P., 1914. — Annélides Polychètes non pélagiques provenant des campagnes de l'Hirondelle et de la Princesse Alice (1885-1910). *Res. Camp. Sci. accomplies sur son Yacht par Albert Ier*, **46** : 1-432.

FAUVEL, P., 1925. — Sur les Ophéliens des côtes de France. *Bull. Soc. Zool. France*, **50** : 77-88.

FAUVEL, P., 1932. — Annelida Polychaeta of the Indian Museum, Calcutta. *Mem. Indian Mus.*, **12** : 1-262.

FAUVEL, P., 1933. — Annélides polychètes du Golfe du Pei Tcheu Ly de la collection du Musée Hoang ho Pai ho, récoltées par le R.P. Leroy, S.J., et le R. P. Licent, S.J. *Publ. Musée Hoang ho Pai ho Tien-Tsin*, **15** : 1-67.

FAUVEL, P., 1936. — Annélides Polychètes du Japon. *Mem. Coll. Sci. Kyoto Imperial Univ., Ser.* 13, **12** : 41-92.

FAUVEL, P., 1941. — Annélides Polychètes de la mission du Cap Horn (1882-1883). *Bull. Mus. natl Hist. nat. Paris, n.s.*, **13** : 272-298.

FAUVEL, P., 1943. — Annélides Polychètes de Californie recueillies par L. Diguet. *Mém. Mus. nat. Hist. nat., n.s.*, **18** : 1-32.

FAUVEL, P., 1953. — *The fauna of India.* The Indian Press Ltd Allahabad, 507 pp.

FOURNIER, J.A. & LEVINGS, C.D., 1982. — Polychaetes recorded near two pulp mills on the coast of Northern British Columbia: a preliminary taxonomy and ecological account. *Syllogeus*, **40** : 1-91.

FUJIWARA, T., 1933. — On a new species of japanese polychaeta *Travisia japonica* sp. nov. *J. Sci. Hiroshima Univ. Zool.*, **2** : 91-103.

GLÉMAREC, M., 1969. — *Les peuplements benthiques du plateau continental Nord-Gascogne.* Thèse Doctorat d'Etat, Université de Brest, 167 pp.

GRUBE, E., 1866. — Neue Anneliden aus den Gattungen *Eunice, Hesione, Lamprophaes* und *Travisia. Jahresber. Schles. Gesells. in Breslau*, **44** : 64-66.

GRUBE, E., 1869. — Familie der Opheliaceen. *Jarresber. Schles. Gesells. Vaterl. Breslau*, **45** : 59-68

HAMOND, R., 1966. — The Polychaeta of the coast of Norfolk. *Cah. Biol. mar.*, **7** : 383-436.

HARRIS, T., 1991. — The occurrence of *Ophelia bicornis* (Polychaeta) in and near the estuary of the River, Exe, Devon. *J. mar. Biol. Ass. U.K.*, **71** : 391-402.

HARTMAN, O., 1938. — Description of new species and new generic records of polychaetous annelids from California of the families Glyceridae, Eunicidae, Stauronereidae and Opheliidae. *Calif. Public. Zool.*, **43** : 93-111.

HARTMAN, O., 1948. — The marine annelids erected by Kinberg with notes on some other types in the Swedish State Museum. *Ark. Zool. Stockholm*, **42** : 1-137.

HARTMAN, O., 1952. — The marine annelids of the United States Navy Antarctic Expedition, 1947-48. *J. Wash. Acad. Sci.*, **42** : 231-237.

HARTMAN, O., 1953. — Non pelagic Polychaeta of the Swedish Antarctic Expedition 1901-1903. *Further Zool. Res. of the Swedish Antarctic Expedition 1901-1903, Stockholm*, **4**, 11: 1-83.

HARTMAN, O., 1959. — Catalogue of the Polychaetous annelids of the world. *Allan Hancock Found. Occ. Papers*, **23** : 1-628.

HARTMAN, O., 1961. — Polychaetous Annelids from California. *Allan Hancock Pacif. Exped.*, **25** : 1-226.

HARTMAN, O., 1963. — Submarine canyons of southern California. Part III. Systematics: Polychaetes. *Allan Hancock Pacific Exped.*, **27** : 1-93.

HARTMAN, O., 1965a. — Deep-water benthic Polychaetous Annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Found. Occas. Pap.*, **28** : 1-378.

HARTMAN, O., 1965b. — Benthic biology of the mainland of california. Sections on Polychaetes. *In: An Oceanographic and Biological Survey of the Southern California Mainland Shelf.* Publication n° 27. State Water quality Control Board, Sacramento, California : 1-232

Source : MNHN, Paris

HARTMAN, O., 1966a. — Quantitative survey of the benthos of San Pedro Basin, Southern California. Part 2. Final results and conclusions. *Allan Hancock Pacific Exped.*, **19** : 187-456.

HARTMAN, O, 1966b. — Polychaeta Myzostomidae and Sedentaria of Antarctica. *Antarctic Res. Ser.*, **7**: 1-158.

HARTMAN, O, 1967. — Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from the antarctic seas. *Allan Hancock Monogr. Mar. Biol.*, **2** : 1-387.

HARTMAN, O., 1969. — *Atlas of sedentariate polychaetes annelids from California*. Allan Hancock Foundation, University of Southern California, 812 pp.

HARTMAN, O., 1978. — Polychaeta from the Weddell Sea quadrant, Antarctica. *Antarctic Res. Ser.*, **26** : 124-223.

HARTMAN, O. & FAUCHALD, K., 1971. — Deep-water benthic Polychaetous Annelids off New England to Bermuda and other North Atlantic areas. Part II. *Allan Hancock Monogr. Mar. Biol.*, **6** : 1-327.

HARTMANN-SCHRÖDER, G., 1971. — Annelida, Borstenwurmer, Polychaeta. *Tierwelt Deutschands*, **58** : 1-594.

HARTMANN-SCHRÖDER, G. & HARTMANN, G., 1980. — Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. teil 4. Die Polychaeten der tropischen Nordwestküste (zwischen Port Samson im Norden und Exmouth im Süden). *Mitt. hamb. zool. Mus. Inst.*, **77** : 41-110.

HARTMANN-SCHRÖDER, G., 1986. — Die Polychaeten der 56 Reise der "Meteor" zu den South Shetland-Inseln (Antarktis). *Mitt. hamb. zool. Mus. Inst.*, **83** : 71-100.

HARTMANN-SCHRÖDER, G. & ROSENFELDT, P., 1989. — Die Polychaeten der "Polarstern" -Reise Ant III/2 in die Antarktis 1984. Teil 2: Cirratulidae bis Serpulidae. *Mitt. hamb. zool. Mus. Inst.*, **86** : 65-106.

HOBSON, K.D. & BANSE, K., 1981. — Sedentariate and Archiannelid polychaetes of British Columbia and Washington. *Can. Bull. Fish. Aquat. Sci.*, **209** : 1-144.

HOLTHE, T., 1977. — The Polychaetous annelids of Trondheimsfjorden, Norway. *Gunneria*, **29** : 1-64.

HUTCHINGS, P. & MURRAY, A., 1984. — Taxonomy of Polychaetes from Hawkesbury River and the Southern Estuaries of New South Wales, Australia. *Rec. Austr. Mus.*, **36**, suppl. 3 : 1-119.

IMAJIMA, M., 1961. — Polychaetous annelids collected off the west coasts of Kamchatka. 1. Notes on species in the collections 1957-58. *Publ. Seto Mar. Biol. Lab.*, **9** : 81-102.

IMAJIMA, M., 1963. — Polychaetous annelids collected off the west coast of Kamchatka. 2. Notes on species found in the collection of 1959. *Publ. Seto Mar. Biol. Lab.*, **11** : 345-372.

IMAJIMA, M., 1964. — Benthic Polychaetes collected by the second cruise of the japanese Expedition of deep seas (JEDS-2). *Bull. natn. Sci. Mus. Tokyo*, **7** : 235-254.

IMAJIMA, M. & HARTMAN, O., 1964. — The Polychaetous annelids of Japan. *Allan Hancock Found. Occas. Pap.*, **26** : 1-452.

JONHSTON, G., 1840. — British Annelids. *Ann. Mag. nat. Hist., ser.* 1, **4** : 368-375.

KINBERG, J.G.H., 1866. — Annulata nova. *Oefv. Svenska Vetensk. Akad. Förh*, **22** : 239-258.

KINBERG, J.G.H., 1910. — *Konglia Svenska Fregatten Eugenies Resa omkring jorden under befäl af C.A. Virgin åren 1851-853. Vetenskapliga Iakttagelser pä Konung Oscar den Förstes befallning utgifna delen. Zoologi. 3. Annulater*. Uppsala and Stocklom, Almquist and Wicksells, 78 pp.

KIRKEGAARD, J.B., 1956. — Benthic Polychaeta from depths exceeding 6,000 m. *Galathea Rep.*, **2** : 63-78.

KRKEGAARD, J.B., 1969. — A quantitative investigation of the central North Sea Polychaete. *Spolia*, **29** : 1-285.

KRKEGAARD, J.B., 1980. — Abyssal benthic polychaetes from the northeast Atlantic ocean southwest of the British Isles. *Streenstrupia*, **6** : 81-98.

KNOX, G.A., 1962. — Antarctic Polychaetes from Mawson. Mac Robertson Land. *Trans. Roy. Soc. Nat. New Zealand, Zool.*, **1** : 343-348.

KUDENOV, J.D., 1975. — Sedentary Polychaeta from the Gulf of California, Mexico. *J. Nat. Hist.*, **9** : 205-231.

KÜKENTHAL, W., 1887. — Die Opheliaceen der Expedition der "Vettore Pisani". *Jena. Z. Naturw.*, **21** : 361-373.

LEVENSTEIN, P.P., 1960. — The quantitative distribution of the Polychaeta in the north western Bering Sea [in russian]. *Trudy Inst. Okeanol., Moscou*, **44** : 104-122.

Source : MNHN, Paris

LEVENSTEIN, P.P., 1961a. — The quantitative distribution of the Polychaeta in the north Pacific [in russian]. *Trudy Inst. Okeanol., Moscou*, **45** : 214-222.

LEVENSTEIN, P.P., 1961b. — Polychaeta in the deep sea area of the Bering Sea [in russian]. *Trudy Inst. Okeanol., Moscou*, **46** : 214-222.

LEVENSTEIN, P.P., 1961c. — New data on the Annelida Polychaeta from the deep waters of Java [in russian]. *Okeanol.* **1** : 136-139.

LEVENSTEIN P.P., 1966. — Polychaeta of the Bering Sea [in russian]. *Trudy Inst. Okeanol., Moscou*, **81** : 3-131.

LEVENSTEIN, P.P., 1970. — Ecology and zoogeography of some Pacific Polychaeta of the family Opheliidae. *Trudy Inst. Okeanol., Moscou*, **88** : 213-226.

LEVENSTEIN, P.P., 1971/72. — Ecology and Zoogeography of some Polychaeta representatives of the abyssal Pacific. *Proc. R.S.E. (B)*, **73**, 18 : 171-181.

LEVENSTEIN, P.P., 1975. — The Polychaetous annelids of the deep sea trenches of the Atlantic Sector of the Antarctic ocean [in russian]. *Tans. P.P. Shirshov Inst. Okeanol.*, **103** : 119-142.

LEVENSTEIN, P.P., 1978. — The Polychaetous annelids from the deep sea pacific antarctic ocean [in russian]. *Trudy Inst. Okeanol., Moscou*, **113** : 73-87.

LOI, T.N., 1980. — Catalogue of the types of polychaete species erected by J. Percy Moore. *Proc. Acad. Nat. Sci. Philadelphia*, **132** : 121-149.

MCINTOSH, W.C., 1879. — On the Annelida obtained during the cruise H.M.S. "Valorous" to Davis Stait in 1875. *Trans. Linn. Soc. London, n.s.*, **1**: 499-511.

MCINTOSH, W.C., 1885. — Report on the Annelida Polychaeta collected by H.M.S. "Challenger" during the years 1873-1876. *Challenger Rep.*, **12** : 1-554.

MCINTOSH, W.C., 1908a. — On the same Families of Annelids in the "Porcupine" expeditions of 1869 and 1870, n° 29. *Ann. Mag. Nat. Hist.*, ser 8, **1** : 383-391.

MCINTOSH, W.C., 1908b. — Notes from the Gatty Marine Laboratory, St Andrews, 29. *Ann. Mag. Nat. Hist. London, ser.* 8, **1** : 373-387.

MCINTOSH, W.C., 1915. — *The British Marine Annelids. Polychaeta. Opheliidae to Ammocharidae*. Vol. **3**, Part 1: 1-368.

MOORE, J.P., 1906. — Additional new species of Polychaete from the north Pacific. *Proc. Acad. Nat. Sci. Phil.*, **58** : 217-260.

MOORE, J.P., 1923. — The Polychaetous annelids dredged by the USS Albatross off the coast of Southern California in 1904. IV Spionidae to Sabellidae. *Proc. Acad. Nat. Sci. Philadel.*, **75** : 179-259.

MOORE, C.C.A., 1930. — Polychaete worms. *Discovery Rep., Cambridge*, **2** : 1-222.

MOORE, C.C.A., 1934. — On a collection of Polychaeta from the coast of China. *Ann. Mag. nat. Hist.*, ser. 10, **13** : 353-380.

MOORE, C.C.A., 1936. — Polychaete worm. II. *Discovery Rep., Cambridge*, **12** : 59-198.

MOORE, C.C.A., 1939. — Polychaeta. British Antarctic Research Expedition, 1929-1931. *Adelaide, Australia. Rep., ser.B (Zoology and Botany)*, **4** : 89-156.

PETTIBONE, M.H., 1954. — Marine Polychaeta worms from Point Barrow, Alaska, with additional record from the North Atlantic and North Pacific. *Proc. U.S. Nat. Hist. Mus.*, **103** (3324) : 203-356.

PETTIBONE, M.H., 1956. — Marine Polychaete worms from Labrador. *Proc. U.S. Nat. Hist. Mus.*, **105** (3361) : 531-584.

RATHKE, H., 1843. — Beiträge zur Fauna Norwegens. *Nova. Acta Acad. Leop. Carol. Nat. Cur. Halle*, **20** : 1-264.

REISH, D.J., 1965. — Benthic Polychaetous Annelids from Bering Chukchi and Beaufort Seas. *Proc. U.S. Nat. Hist. Mus.*, **117** (3511) : 131-158.

REISH, D.J., 1968. — A biological survey of Bahia de Los Angeles: gulf of California. Mexico II. Benthic Polychaetous annelids. *Trans. San Diego Soc. Nat. Hist.*, **15** : 67-106.

RETIÈRE, C., 1968. — Contribution à l'étude écologique de la macrofaune annélidienne de la plage de Lancieux (Côtes du Nord). *Bull. Mar. Lab. Dinard*, **1** : 1-59.

Source : MNHN, Paris

RETIÈRE, C., 1971. — Données sur l'écologie de la Polychète *Travisia forbesii* Johnston 1840 (Opheliidae) dans la région de Dinard : mise en évidence du cycle biologique. *C. R. Acad. Sci. Paris*, **272**, *sér D* : 3075-3078.

RETIÈRE, C., 1972. — Structure et dynamique d'une population de *Travisia forbesii* Johnston 1840 (Opheliidae) dans la région de Dinard. *C. R. Acad. Sci. Paris*, *275*, *sér D* : 1543-1546.

RIOJA, E., 1944. — Estudios anelidologicos. II. Estudios de algunos poliquetos del Museo Argentino de ciencias naturales. *An. Inst. Biol. Univ. Mex.*, **15** : 115-138.

RIOJA, E., 1946. — Estudios de algunos poliquetos del Museo Argentino de ciencias naturales. *An. Mus. Argent. B. Aires*, **42** : 39-58.

RISER, N.W., 1987. — Observations on the genus *Ophelia* (Polychaeta Opheliidae) with the description of a new species. *Ophelia*, **28** : 11-29.

ROZBACZYLO, N., 1985. — Los Anelidos poliquetos de chile. *Monografias Biologicas*, **3** : 1-284.

SAINT-JOSEPH., A. de, 1898. — Les Annélides polychètes des côtes de France (Manche et Océan). *Ann. Sci. Nat. Paris, sér. 8*, **5** : 209-464.

SANTOS, S., 1977. — A new species of *Travisia* (Polychaeta, Opheliidae) from Tampa Bay, Florida. *Proc. Biol. Soc. Wash.*, **89** (49) : 559-564.

STÖP-BOWITZ, C., 1945. — Les Ophéliens Norvégiens. *Medd. zool. Mus. Oslo*, **52** : 1-61.

STÖP-BOWITZ, C., 1948. — Sur les Polychètes arctiques des Familles Glycériens, des Ophéliens, des Scalibrégmiens et des Flabelligériens. *Tromsö Mus. Arshefter*, **66** : 1-58.

TREADWELL, A.L., 1914. — Polychaetous annelids of the pacific coast in the collection of the Zoological Museum of the University of California. *Univ. Calif. Publ. Zool.*, **13** : 175-234.

UEBELACKER, J.M., 1984. — Chapter 17. Opheliidae. *In* : J.M. UEBELACKER & P.G. JOHNSON (eds.), *Taxonomic guide to the polychaetes of the northern Gulf of Mexico*. Vol. III. Bary A. VITTOR & Associates, Inc., Mobile, Alabama **7** : 1-15.

UCHIDA, H., 1967. — Polychaetous annelids from Shakotan. (Hokkaido). I. The collection in 1967. *J. Fac. Sci. Hokkaido Univ. (Zool.)*, **16** : 595-612.

USCHAKOV, P.V., 1955. — Polychaeta of the Far Eastern seas of the USSR [In russian]. *Akad. Nauk SSSR. Zool. Inst., Opred. po faune SSSR*, **56**: 1-445.

VERRILL, A.E., 1873. — Report upon invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *Rep. U.S. Commissioner Fish.*, 1871-1872: 295-778.

WESENBERG-LUND, E., 1950. — Polychaeta. *Danish Ingolf Exped.*, **4**, 14 : 1-92.

WESENBERG-LUND, E., 1951. — Polychaeta. *The Zoology of Iceland*, **2**, 19 : 1-182.

WILEY, E.O., 1981. — *Phylogenetics. The theory and practice of Phylogenetic Systematics*. J. Wiley and Sons, New York, 439 pp.

WOLFF, W.J., 1973. — The estuary as a habitat : an analysis of data on the soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Sheldt. *Zool. Verhandel. Leiden*, **126** : 1-242.

Source : MNHN, Paris

# A new Species of *Ophryotrocha* (Polychaeta, Dorvilleidae) associated with Ice Scours in the Canadian Arctic Archipelago

*Judith A. FOURNIER & Kathleen E. CONLAN*

Invertebrate Zoology, Collections and Research Division
Canadian Museum of Nature/Musée canadien de la nature,
C.P./P. O. Box 3443, Station/Succ. "D"
Ottawa, Ontario Canada, K1P 6P4

ABSTRACT

*Ophryotrocha spatula* sp. n. is described from ice scours off Cornwallis Island in the Canadian Arctic Archipelago. This species resembles *O. scarlatoi* Averincev, 1989 in having the last 5-12 setigers laterally prolonged into a broad, lobulate flange but differs from this species in the structure of the jaw apparatus and setae and in possessing ventral parapodial cirri and a median anal cirrus.

RÉSUMÉ

**Une nouvelle espèce d'*Ophryotrocha* (Polychète, Dorvilleidae) associée aux sillons d'icebergs dans l'Archipel arctique canadien**

Le polychète *Ophryotrocha spatula* sp. n. en provenance de sillons d'icebergs près de Cornwallis Island dans l'Archipel arctique canadien est décrit. Cette espèce ressemble à *O. scarlatoi* Averincev 1989, par ses bords dorsaux des 5-12 sétigères postérieurs élargis en forme de lobe membraneux, mais elle s'en distingue par les soies, la forme des mâchoires, et la présence de cirres ventraux parapodiaux et un cirre médian anal.

## INTRODUCTION

A joint Canadian/United States team has been studying scour formations caused by grounded multi-year ice off the coast of Cornwallis Island, Northwest Territories in the Canadian Arctic Archipelago (Queen Elizabeth Islands). Icescouring is probably the most disruptive and widespread physical disturbance to marine bottom communities in polar waters. In the Arctic, pressure ridges of ice scour the sea floor to depths of 60 m and larger icebergs ground as deep as 750 m (LEWIS & BLASCO, 1990). The team has been investigating the

FOURNIER, J. A. & K.E. CONLAN, 1994. — A New Species of *Ophryotrocha* (Polychaeta, Dorvilleidae) associated with Ice Scours in the Canadian Arctic Archipelago. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 185-190. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

benthic population and community responses to ice scour, documenting the successional stages of biotic recovery in order to determine whether widespread patterns of zonation and larger spatial and temporal community mosaics are correlated to the disturbance.

An undescribed dorvilleid of the genus *Ophryotrocha* was among the most abundant polychaete species and showed a strong positive association with the disturbed sediments of the ice scours and berms. Mature specimens of this species have the dorsal surface of the last 5-9 segments laterally prolonged into a lobulated spoon-shaped flange. The species resembles *Ophryotrocha scalatoi* Averincev, 1989 from Franz-Joseph Land and Norway (OUG, pers. comm.) but differs in details of jaw dentition and the presence of ventral parapodial cirri, most noticeable in the posterior segments.

## METHODS

Samples were collected by Hunter S. LENIHAN and Kathleen E. CONLAN using diver-operated hand cores pressed into the sediment. Six cores were collected from locations inside and outside each scour and from the scour berm itself for a total of 18 samples from each of four scours. The 72 samples yielded a total of 551 specimens of the new species.

Samples were screened through a 0.5 mm mesh, fixed in 4 % formaldehyde solution and later transferred to 70 % ethanol. Final sorting was done in the laboratory under a dissection microscope. Specimens were examined under dissection and phase-contrast compound microscopes. Drawings were done with a drawing tube. Ocular micrometers in both compound and dissecting microscopes were used for measurements. Body width measurements do not include parapodia.

## DESCRIPTION OF COLLECTION SITES

Ice Scour 1 : Cape Martyr, Cornwallis Island, 74°41' N, 95°06' W, depth 15 m; outside scour (one specimen), scour berm (18 specimens), inside scour (27 specimens) sampled 31 July 1991. Outside of scour had gravel/cobble substrate over silt, little *Laminaria* cover, exposed to frequent strong currents. Scour was perpendicular to shoreline, 3-4 m wide, 1.5-2 m deep into sediment, more than 40 m long, estimated age less than one year, probably produced during spring breakup of ice. Sediment inside scour loose and very soft, 4-5 cm oxic layer covering grey anoxic zone. Scour berm with 7-8 mm oxic layer covering sediment. Epifauna outside scour comprised very abundant echinoderms (ophiuroids, echinoids, asteroids, holothuroids), bivalves (*Mya truncata* L., *Serripes groenlandicus* (Bruguière), *Astarte borealis* (Schumacher)) and soft corals (*Gersemia* sp.).

Ice Scour 2: Assistance Bay, Cornwallis Island, 74°39' N, 94°18' W, depth 7 m; outside (31 specimens), scour berm (157 specimens) and inside (94 specimens) sampled 2 August 1991. Scour parallel to shore line in semi-protected bay, well flushed by strong currents and river flow. Scour estimated to have formed within previous 24 hours, about 6 m wide, 0.5 m deep and over 50 m long. Scour bottom hard with very little loose sediment over large cobbles. Scour berm 5-10 cm high with stones and cobble. No epifauna visible within scour.

Ice Scour 3 : Resolute Bay, Cornwallis Island, 74°41' N, 94°50' W, depth 10 m; outside scour (zero specimens) sampled August 4, 1991, scour berm (125 specimens) and inside (44 specimens) 8 August 1991. Circular "crater" in area of 40-60 % *Laminaria* cover, estimated to have formed in previous 48 hours, more than 25 m in diameter, 0.25 m deep to hardpan. Berm 2-2.5 m high.

Ice Scour 4: Resolute Bay, Cornwallis Island, 74°41' N, 94°50' W, depth 7 m; outside (1 specimen) scour berm (51 specimens), and inside (two specimens), 8 August 1991. Scour estimated to have formed within previous 48 hours, about 30 m long, 3 m wide, cut to hardpan, 0.25 m deep. Berm about 1 m high, loose sediment with stones and gravel. Pockets of anoxic sediment along length of trough. Only a few *Buccinum* sp. seen within scour, *Mya* spp. and *Macoma* spp. on berm.

Resolute Bay is protected by a sill at the entrance. Bottom was fine sediment and cobble, about 20 cm deep, over a hardpan base that prevented bivalves such as *Mya* spp. and *Serripes groenlandicus* from burrowing deeper. Scours 3 and 4 were in the central part of the bay, close to shore, in an area of dense *Laminaria* cover.

Source : MNHN, Paris

## SYSTEMATICS

### *Ophryotrocha spatula* n. sp.

MATERIAL EXAMINED. — Holotype: CMNA1993-0046, mature specimen, 3.7 mm long, 0.5 mm wide anteriorly, flange 0.8 mm across at widest point. Type Locality: Assistance Bay, Cornwallis Island, Ice Scour 2, Core 2, scour berm, 7 m depth, collected 2 August 1991.

Paratypes: CMNA1992-0158, 79 specimens, remainder of sample from scour berm, core 2, Ice Scour 2, Assistance Bay, Cornwallis Island.

An additional 471 specimens have been found in the rest of the samples (Table 1).

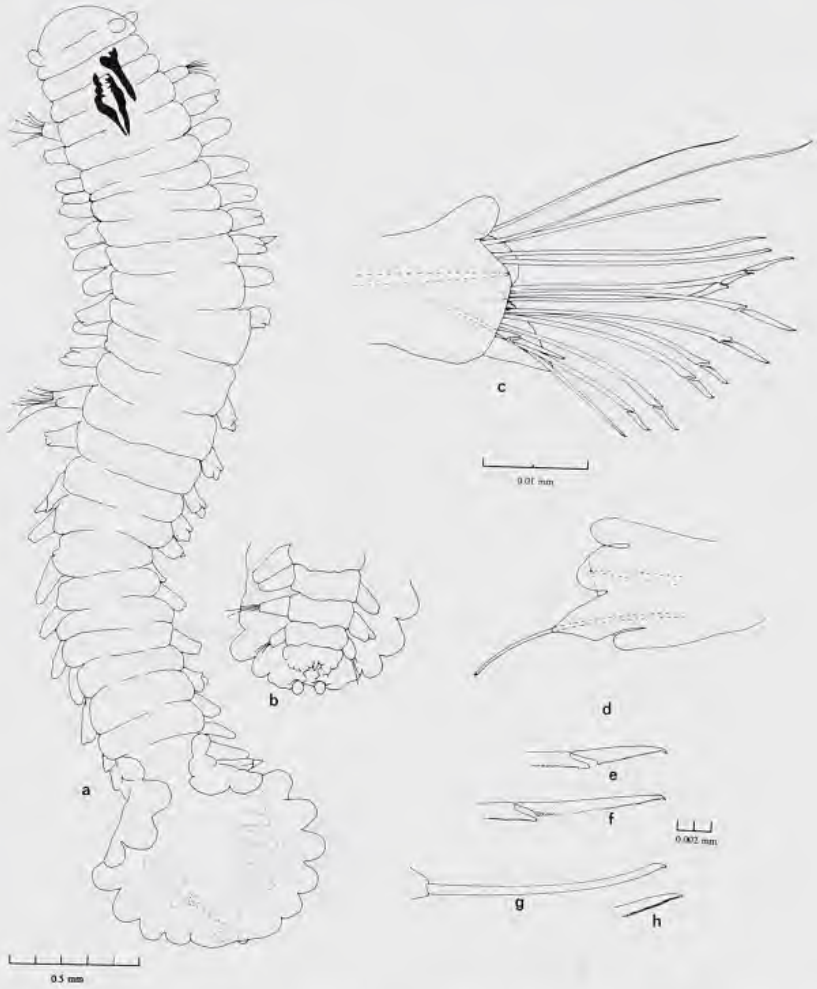



FIG. 1. — a. *Ophryotrocha spatula* sp. n., dorsal view, holotype, most setae omitted. b. Paratype, ventral view, posterior. c. Paratype, anterior view of median parapodium. d. Posterior view of posterior parapodium, setae omitted except for ventral simple seta. e, f. Long and short blades of compound falcigers. g. Ventral simple seta. h. Tip of simple seta.

Source : MNHN, Paris

SPECIES DIAGNOSIS. — Medium-sized *Ophryotrocha*, 3.7 to 5.5 mm long for 25-43 setigers, anterior body width about 0.5 mm, dorsum of posterior 5-12 segments laterally expanded into a lobulate flange (Fig. 1a). Prostomium with 1 pair each palps and antennae, ovate. Single pair of small eyes usually visible on posterior margin of prostomium. Jaw apparatus (Fig. 2) darkly sclerotized, mandibles rod-like with toothed, bifid anterior margin, forceps P-type, inner edge with one row of about 10 large teeth interspersed with smaller ones and secondary ridge with many fine teeth. Free denticles seven pairs in two groups. Parapodia with both dorsal and ventral cirri, former difficult to discern in anterior parapodia. Supra-acicular setae simple unidentate blades with very finely serrated edges. Sub-acicular setae compound, unidentate blades with very finely serrated edges, varying in length by factor of two. Pygidium flattened, anal cirri ovate, inserted ventrally. Anus ventral or terminal depending on state of dilation, bearing mid-ventral papilla.

DESCRIPTION OF HOLOTYPE. — Holotype (Fig. 1a) 3.7 mm long for 32 setigers, body width 0.5 mm anteriorly, 0.8 mm at widest point of posterior flange. Colour in alcohol off-white. Body sparsely ciliated but setigerous segments have extensive glandular regions covering dorsum.

Prostomium rounded, bearing two small ovate antennae dorsally and pair of ventral palps almost identical in size and shape. Eyes not visible.

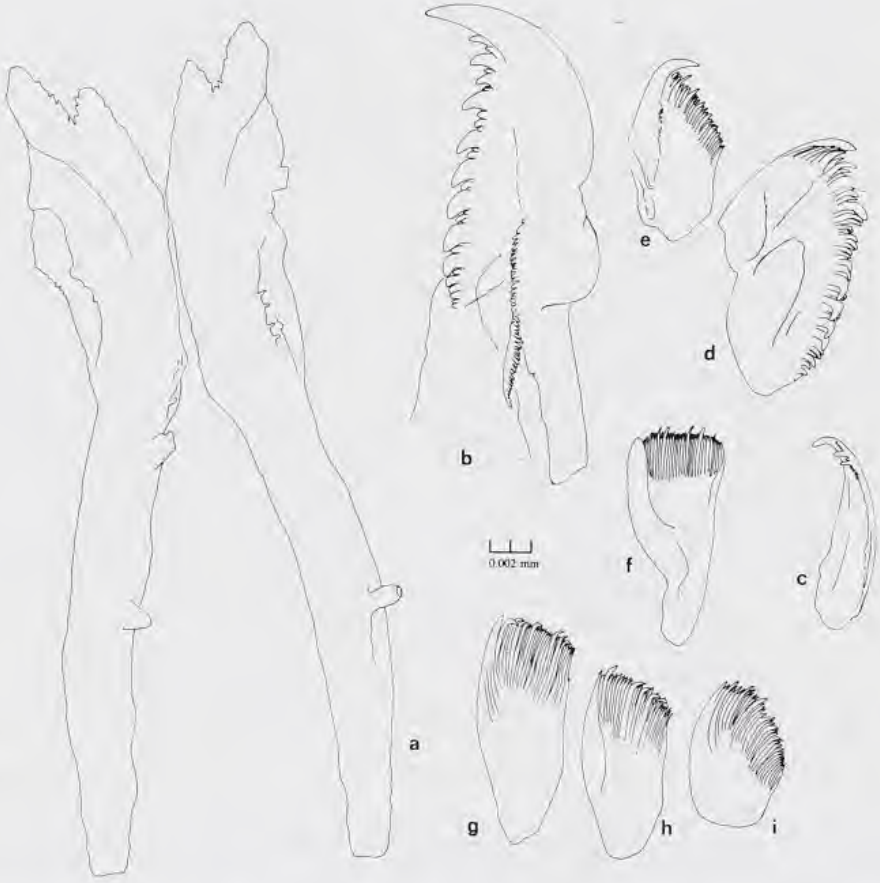



FIG. 2. — *Ophryotrocha spatula* sp. n., jaw apparatus from paratype. a. Mandibles. b. Forceps (base broken). c, d, e. First group of free denticles. f, g, h, i. second group of free denticles.

Peristomium followed by achaetous apparent first segment. Mouth parts (Fig. 2) darkly sclerotized. Forceps and free denticles forming separate group. Mandibles (Fig. 2a) partially protruding, rod-shaped with jagged bifid

Source : MNHN, Paris

leading edge and several unpaired, irregular protrusions along length of shaft. Forceps (Fig. 2b) P-type (HILBIG & BLAKE, 1991) with single main tooth, inner edge with row of about 10 large teeth interspersed with at least 20 smaller ones, secondary median ridge bearing row of much finer teeth; main shaft darkly sclerotized but surrounded by thin flange.

Free denticles, seven pairs arranged in two primary groups (Fig. 2c-i). Denticles closest to the forceps (Fig. 2c-e) dark and strongly toothed; median member (Fig 2c) fang-shaped. Outer denticles (Fig. 2f-i) thin and broad with numerous long slender teeth interspersed with several stouter ones.

Parapodia uniform in shape; setae vary only in number. Dorsal and ventral cirri ovate but latter very difficult to distinguish in anterior setigers. Presetal lobe truncate. Dorsal postsetal lobe rounded; ventral, retractile lobe triangular and supported by single simple seta that resembles secondary emergent acicula (Fig. 1c-d). Aciculae very long and stout, seated proximally against row of longitudinal muscle group. Supra-acicular setae simple, unidentate flattened blades with very finely denticulate lower margin (Fig. 1, c-g-h). Second superior seta longer than others. Subacicular setae compound falcigers with blades varying in length by factor of two, unidentate with very finely denticulate border, almost identical to supra-acicular setae in size and form.

Setiger 1 with one supra-acicular seta, three compound falcigers and one subacicular simple ventral seta. Following setigers with four supra-acicular setae, six compound falcigers and one ventral simple seta. Last setiger with two simple supra-aciculars, two compound falcigers and one ventral seta. Large specimens have more setae per bundle but pattern invariable.

Last 9 setigers expanded into broad, spatulate flange (Fig. 1a), free from dorsal cirri which project freely from below flange, (Fig. 1b).

Pygidium flattened with two ovate anal cirri inserted ventrally (Fig. 1b). Anus ventral with opening occupying ventral surface of last three setigers; stout ventral median papilla.

OTHER SPECIMENS. — Mature specimens reach 5.5 mm with 25 to 43 setigers. No direct linear relationship found between body length and number of setigers. Many specimens with adhering sand grains and fine clay particles. While all were off-white in colour, a few of the largest specimens had yellowish-brown tinge. Most specimens have single pair of small eyes on posterior margin of the prostomium, usually covered by part of peristomium. Posterior flange often curled dorsally, forming a cylinder. Some of largest specimens show little expansion, other smaller ones, such as the holotype, almost double body width. Not all specimens have anal opening as extended as holotype; it is sometimes contricted and terminal as illustrated in Figure 1b.

No gametes found in the holotype or any of the other specimens examined, including the largest. A few juveniles, about 2 mm long for 20 setigers, are present in the samples but all appear to be damaged. The jaw apparatus shows obvious similarities to the adults but the posterior flange is not developed. Instead, the body appears to terminate in an undifferentiated, asetigerous region. These specimens need more study.

ETYMOLOGY. — The species name *spatula* is Latin for spoon and refers to the diagnostic unique structure of the posterior segments.

COMPARISON TO OTHER SPECIES OF *Ophryothrocha*. — The extensive review of HILBIG & BLAKE (1991) provided a table of characters of most of the known species in the genus but overlooked *O. scarlatoi* Averincev, 1989 which also has a broad posterior flange. This species was only superficially described and figured. OUG (in prep.) has discovered several specimens from Norway that resemble *O. scarlatoi*. These differ from the present specimens in having longer mandibles, in details of the maxillae and setae, and in lacking ventral parapodial cirri and a median anal papilla. It will be necessary to re-examine the types of *O. scarlatoi* in order to determine whether we are dealing with one, two or three species or subspecies. Attempts to borrow the type specimens of *O. scarlatoi* have been unsuccessful (E. OUG, pers. comm.).

The parapodia and setae of *O. spatula* resemble those of *O. puerilis siberti* (McIntosh, 1885) as illustrated by GEORGE & HARTMANN-SCHRÖDER and HARTMANN-SCHRÖDER (1985). The parapodia are not as strongly lobed as those of *O. lobifera* Oug, 1978 but that species also has "*puerilis*-type" setae. Although HILBIG & BLAKE (1991) do not tabulate the presence/absence of anal cirri and papillae, there are species which lack anal cirri (*O. paralabidion* Hilbig & Blake, 1991; *O.* sp. near *scarlatoi* Oug), species with cirri reduced to "thread-like" appendages (*O. bacci* Parenti, 1961; *O. geryonicola* (Esmark, 1874), species with the anus dorsal (*O. lobifera* Oug, 1978), and species with a ventral papilla as well as anal cirri (*O. longidentata* Josephson, 1975; *O. maculata* Åkesson, 1973; *O. minuta* Levi, 1954; *O. puerilis siberti* (McIntosh, 1885)). It is possible that the presence of a ventral papilla has been overlooked in other species.

Source : MNHN, Paris

TABLE 1. — Distribution of *Ophryotrocha spatula* sp. n., pooled totals of six samples each collected from outside, the berm and inside four different ice scours off Cornwallis Island, Canadian Arctic Archipelago.

| Scour Number | Outside Scour | Berm | Inside Scour |
|---|---|---|---|
| N° 1, Cape Martyr, 15 m | 1 | 18 | 27 |
| N° 2, Assistance Bay, 7 m | 31 | 157 | 94 |
| N° 3, Resolute Bay, 10 m | 0 | 125 | 44 |
| N° 4, Resolute Bay, 7 m | 1 | 51 | 2 |
| Total | 33 | 351 | 167 |
| Mean | 8.25 | 87.75 | 41.75 |
| Standard Deviation | 13.14 | 55.67 | 33.66 |

## DISTRIBUTION

*Ophryotrocha spatula* sp.n. is known only from the shallow waters of Barrow Strait off Cornwallis Island. It shows a strong affinity for the disturbed sediments of ice scour berms or troughs as opposed to the compacted sediment outside the scour (Table 1). It was much more abundant on fresh scours (2, 3, and 4) than the older scour (1). Analysis of distribution against grain size (mean ø) failed to demonstrate a significant relationship ($r^2 = 0.255$).

## ACKNOWLEDGEMENTS

The authors are grateful to Diana LAUBITZ, Collection Manager, Invertebrate Zoology for facilitating our collaboration on this project and for her constructive criticism of the manuscript. We thank Hunter LINIHAN, Brenda KONAR, and staff of Moss Landing Marine Laboratories, California, and Buster WELCH of the Department of Fisheries and Oceans, Resolute Marine Laboratory for assistance in the field and laboratory Ed HENDRYKS helped with specimen sorting. François GÉNIER, Michel GOSSELIN and André MARTEL corrected the French title and text.

## REFERENCES

AVERINCEV, V.G., 1989. — Sezonnaya dinamika polikhet vysokoarkticheskikh pribrezhnykh ekosistem Zemli Frantsa-Iosifa (Errantia). [Seasonal dynamics of polychaetes from the high Arctic coastal ecosytem of Franz-Joseph Land (Errantia).] Akademiya Nauk SSSR. *Apatity* : 1-78. (in Russian).

GEORGE, J. D., & G. HARTMANN-SCHRÖDER, 1985. — Polychaetes: British Amphinomida, Spintherida and Eunicida. *Synop. Brit. Fauna* (New Series), **32** : 1-221.

HILBIG, B. & J.A. BLAKE, 1991. — Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with a generic revision of *Ophryotrocha*. *Zool. Scri.*, **20** (2) : 147-184.

LEWIS, C.F.M., & S.M. BLASCO, 1990. — Character and distribution of sea-ice and iceberg scours : keynote address. *In*: J.I. CLARK (ed), *Workshop on ice scouring and the design of offshore pipelines*, Calgary, Alberta, April 18-19, 1990. Canada Oil and Gas Lands Administration, Energy, Mines, and Resources Canada : 57-101.

OUG, E., 1978. — New and lesser known Dorvilleidae (Annelida: Polychaeta) from Scandanavian and northeast American waters. *Sarsia*, 63 : 285-303.

Source : MNHN, Paris

# Two new species of *Branchiomma* (Sabellidae) with redescriptions of closely related species and comments on *Pseudobranchiomma* and *Sabellastarte*

*Phyllis KNIGHT-JONES*

School of Biological Sciences
University of Wales
Swansea U.K.

ABSTRACT

Species of *Branchiomma* Kölliker (= *Dasychone* Sars) are reviewed briefly in order to describe two new species, *B. moebii* from the Mediterranean and *B. spongiarum* from the Faroe Islands. Figures of *Branchiomma infarctum*, *B. bahusiense* and *B. arcticum* (= *Sabellastarte arctica*) are given for comparison. SEM helps to show (a) specific differences in uncini and (b) differences between the stylodes of *Branchiomma* and the "reduced stylodes" of *Pseudobranchiomma* Jones. *Pseudobranchiomma* should include some species formerly in the genera *Branchiomma* and *Sabellastarte* Krøyer.

RÉSUMÉ

**Deux nouvelles espèces de *Branchiomma* (Sabellidae) avec des redescriptions des espèces voisines et des remarques sur *Pseudobranchiomma* et *Sabellastarte***

Les espèces de *Branchiomma* Kölliker (= *Dasychone* Sars) sont passées en revue brièvement pour décrire deux espèces nouvelles, *B. moebii* de Méditerranée et *B. spongiarum* des îles Féroé. Des figures des *Branchiomma infarctum*, *B. bahusiense* et *B. arcticum* ( = *Sabellastarte arctica)* sont données pour comparaison. L'observation au SEM permet de voir a) les différences spécifiques entre les uncini et b) les différences entre les stylodes de *Branchiomma* et les "stylodes réduits" de *Pseudobranchiomma* Jones. *Pseudobranchiomma* comprend quelques espèces placées autrefois dans les genres *Branchiomma* et *Sabellastarte* Krøyer.

## INTRODUCTION AND METHODS

Collections from the Mediterranean (KNIGHT-JONES *et al.*, 1991) and the Faroes (KNIGHT-JONES, 1993) yielded several species of *Branchiomma* as diagnosed by JOHANSSON (1927) and FITZHUGH (1989). Most species were difficult to name, as descriptions are often inadequate and JOHANSSON's review was partial. It was therefore

---

KNIGHT-JONES, P., 1994. — Two new species of *Branchiomma* (Sabellidae) with redescription of cloesely related species and comments on *Pseudobranchiomma* and *Sabellastarte*. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 191-198. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

necessary to study types (or original material) of all known *Branchiomma* species. It soon became clear that many synonyms in the literature were incorrect. Two new species are compared here with those that are morphologically most similar and *B. bahusiense* is figured for the first time. Some species are close to *Pseudobranchiomma* Jones (1962), so *Pseudobranchiomma emersoni* Jones was also studied and compared with *Branchiomma* and *Sabellastarte*.

Material has not yet been found of species followed here by asterisks, but these were figured in the original descriptions. All other listed species have been examined and will be compared elsewhere. Original citations of most species listed here can be found in HARTMAN, 1959, under *Branchiomma*, *Dasychone*, or *Sabella*.

Optical microscopy was helped by a Wild drawing attachment. For scanning electron microscopy (KNIGHT-JONES & FORDY, 1979) alcohol preserved material was washed in distilled water, placed in a weak cleaning solution (Decon 75) in an ultrasonic bath for 20-30 sec, rinsed in distilled water, dehydrated in an acetone series, coated in a polaron MK2 sputter coater, and examined in a JEOL 35 C. Crown radioles were transferred before coating to a Polaron MK1 critical point drying unit using $CO_2$ as the intermediate liquid. Fascicles of chaetae were also studied by SEM but no specific differences in surface detail could be found.

## OLD AND NEW SPECIES OF *BRANCHIOMMA*

*Branchiomma bombyx* (Dalyell), *B. lucullanum* (delle Chiaje), *B. violaceum* (Schmarda), *B. natalense* (Kinberg), *B. capense* (McIntosh) and *B. pseudoviolaceum* (Augener) have their dorsal collar margins fused to the edges of the narrow faecal groove, but the two new species described here are like most *Branchiomma* in having free dorsal margins separated by a wide gap. Their uncinal crests have many rows of teeth, as in *Branchiomma infarctum* (Krøyer = *Dasychone decora* Sars), *B. inconspicuum* (Sars), *B. bahusiense* Johansson (as *B. infarcta var. bahusiensis* ) and *B. arcticum* (Ditlevsen = *Sabellastarte arctica* Ditlevsen) with which they are compared.

The radioles of the new species lack the 'macrostylodes' (defined as being three or more times the length of neighbouring pairs, see KNIGHT-JONES *et al.*, 1991), which are seen in distal halves of dorsal and lateral radioles in *B. nigromaculatum* (Baird) (= *Sabella crispa* Krøyer; = *Dasychone ponce* Treadwell), *B. boholense* (Grube), *B. bairdi* (McIntosh), *B. japonicum* (McIntosh), *B. conspersum* (Ehlers) (= ? *Dasychonopsis arenosa* Treadwell), *B. maculatum* (Fischli)*, *B. gravelyi* (Aziz)*, *B. loandense* (Treadwell) and *B. pererai* de Silva (as *B.cingulata var. pererai*) [some of the latter four species may be synonyms of the others]. Some species which lack distal macrostylodes, e.g. *B. havaiicum* (Kinberg), *B. cingulatum* (Grube), *B. luctuosum* (Grube), *B. curtum* (Ehlers), *B. corolliferum* (Ehlers) and *B. galei* (Augener), differ from the two new ones in having thoracic uncinal crests with just two or three rows of few teeth (e.g. Fig. 4g-h). At least the last five of these are distinct species and will be described elsewhere.

***Branchiomma moebii*** *sp. nov.*— Holotype ZMHUB 2304a (Fig. 1a-d, f-k); paratype ZMHUB 2304b (Fig. 1e) Rovinj, N Adriatic.
*Dasychone lucullana* — SAINT-JOSEPH, 1906 : 241. Cannes (MNHNP A311). *Branchiomma* species A.— KNIGHT-JONES *et al.*, 1991 : 847. One specimen found in gulley 3-13 m deep SW of Harem point, Bodrum, Turkey (personal collection).

Additional material: a single specimen from the Bay of Muggia, Trieste (ZMUC), labelled *D. lucullana* by MARENZELLER.

The following description is based on the holotype, data in parentheses refer to the paratype.

Body 19 by 3.5 (17 by 3) mm with 40 (50) segments of which 8 are thoracic; crown a further 19 (14) mm long, ventrally involuted at base; radioles 16 (18) on each side connected by a shallow web; each with about 25 (18) pairs of tongue shaped stylodes, larger pairs towards bases of dorsal and lateral radioles (Fig. 1c-d); radiolar eyes almost obscured by narrow dense pigment bands lying just anterior to bases of (usually) alternate pairs of stylodes (Fig. 1d), but eyes not apparent in paler, more distal bands or areas between bands (more eyes occur in Bodrum material -see below); apinnulate tips of radioles fine, 1 or (less commonly) 2 mm long; dorsal lips tapered, grooved (with midrib support), about a quarter of length of crown and with fairly narrow lamellae, the dorsal lamella attached to base of adjacent radiole, without pinnular support; collar with dorsal gap, small ventral lappets and no ventro-lateral notches; 1st segment (excluding collar margin) about same length as others in thorax

Source : MNHN, Paris

(measured at sides); thoracic fascicles (segments 2 to 8) with about 10 superior chaetae which are slender and scarcely geniculate, the 'knee' region scarcely wider than shaft (Fig. 1g), and about 20 inferior geniculate chaetae with knee up to twice width of shaft (Fig. 1h); thoracic uncini with an extensive crest of small compact teeth (Fig. 4a-b) not usually seen in light microscopy (Fig. 1f); thoracic tori long (segment 7 with about 30 uncini), all but the first two tori reaching ventral shields; most fascicles of abdominal chaetae forming compact tufts, outer chaetae geniculate (Fig. 1k) with thick emergent shafts arranged in a C-shape (see Fig. 1a, insert) around a cluster of capillary chaetae (Fig. 1j); pigment patterns dark brown, most thoracic ventral shields with two D-shaped patches, 1st shield with paired transversely elongate triangles, dorsal side of thoracic parapodia and inter-ramal area (between fascicles and tori) with unusually large patches, and dorsal side of abdominal parapodia with dark triangles.

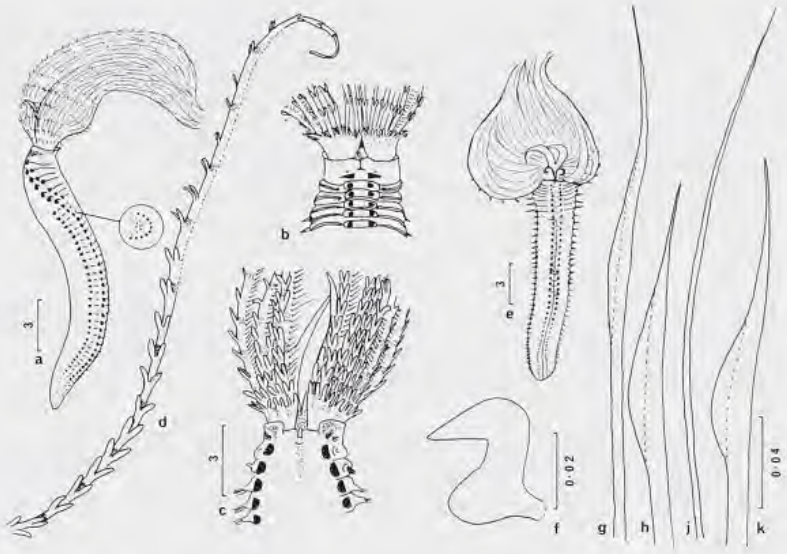



FIG. 1. — *Branchiomma moebii sp. nov.*: a, lateral view of holotype. — b, ventral thorax. — c, dorsal thorax. — d, whole radiole. — e, ventral view of paratype. — f, thoracic uncinus. — g, superior thoracic chaeta from 7th thoracic fascicle. — h, same, but inferior thoracic chaeta. — j, superior capillary chaeta from 6th abdominal fascicle. — k, same, but inferior chaeta. Scales in mm: b as c; g, h, j as k.

This species is named after Professor K. A. MÖBIUS (1825-1908) who collected the largest and best preserved specimens. He, CLAPARÈDE & MARENZELLER labelled their material *Dasychone lucullana*, but the dorsal lips of that species are short (lengths only two times breadth, KNIGHT-JONES *et al.*, 1991) and the dorsal collar margins are fused to the sides of the faecal groove.

On the Bodrum specimen some stylodes next to the web are unpaired, the more basal stylodes from dorsal and lateral radioles are less crowded (more like those of paratype) and eyes are present between most successive pairs of stylodes. Eyes not associated with colour bands, however, are smaller with fewer ocular units. Eyes are absent near the base of the crown (as in Rovinj material) and between a few other random pairs of stylodes. Frequency of radiolar eyes was not noted in the material from Cannes and Trieste.

The following four species are the only ones within *Branchiomma* which resemble *B. moebii* in having widely separated dorsal collar margins and uncinal crests with numerous small teeth:

- *Branchiomma infarctum* (Krøyer, holotype 'Greenland?', ZMUC, Fig. 2a-d, j-k) has stylodes like those of *B. moebii* (cf. Figs 1d; 2e), but larger specimens of *B. infarctum* (e.g. MALMGREN, 1866, NRS 1252, Fig. 2f-g) have broader, almost subcircular stylodes towards the bases of the dorsal and lateral radioles. Like *B. moebii*, *B. infarctum* is plump (body length 4 to 5 times breadth, thorax about as long as broad, with crown up to three quarters of body length), but *B. infarctum* differs in having 1) a more extensive collar (especially ventrally) with ventro-lateral notches, 2) very numerous chaetae (about 80 in both thoracic and abdominal fascicles), 3) posterior

Source : MNHN, Paris

inferior thoracic chaetae more slender ('knee' scarcely wider than shaft Fig. 2k), 4) thoracic uncini with a longer neck (cf. Figs 2h, j; 1f), 5) no radiolar eyes and 6) no pigment pattern other than bands on crown and indistinct inter-ramal spots. Many records of *infarctum* (e.g. LEVINSEN, 1886; DITLEVSEN, 1937; BERTELSEN, 1937; ZMUC) are in fact the more elongate species *Branchiomma arcticum*.

- *Branchiomma arcticum* (Ditlevsen = *Sabellastarte arctica* Ditlevsen, holotype, Baffin Bay "Godthaab Expd". Stn 86 ZMUC) has similar stylodes to *B. moebii* (these had been overlooked by Ditlevsen, as most of his description referred to specimens from station 166, that had suffered histolysis, ZMUC) but differs from *B. moebii* in having 1) an elongate shape (crown normally 0.25 to 0.4 of body length), 2) first segment about twice the length of the following one (measured at sides), 3) prominent ventral collar lappets (Fig. 2t & w, specimens preserved out of and in tubes respectively), 4) tori with gaps between their ventral ends and ventral shields, and 5) uncini with broader crests of more distinct teeth (Fig. 4e).

- *Branchiomma bahusiense* Johansson (syntypes from W Sweden, ZMUU 346 a-b; other material from SE Faroes, NHMT, KNIGHT-JONES 1992) is like *Branchiomma moebii* in having a plump body and a crown usually more than half body length (Fig. 2q), but differs in having 1) no radiolar eyes, 2) narrower stylodes; 3) collar with prominent ventral lappets; 4) short tori not reaching ventral shields (Fig. 2p); 5) broader thoracic uncini with fewer crest teeth (Fig. 4f) and a longer neck (cf Figs 1f; 2s); 6) more quadrangular, less distinct pigment blotches on the ventral shields (Fig. 2p), and 7) much smaller inter-ramal spots.

- *Branchiomma inconspicuum* (M. Sars, in G. O. Sars, as *Dasychone* ZMUO) has uncini which seem to be like those of *B. moebii* but, unlike *moebii*, has prominent ventral collar lappets and no colouration except tiny inter-ramal spots.

***Branchiomma spongiarum*** *sp. nov.* — Holotype ZMUC, Fig. 3, paratype NHMT, both from Stn 377 (BIOFAR Survey) lat. 61°43'53" N, long. 05°42'77" W, depth 274 m. - SE of Faroes.
*Branchiomma sp.* — KNIGHT-JONES, 1992, Faroes shelf (NHMT).

Additional BIOFAR records : Stn. 27, 61°54'10 N, 05°03'80 W, 225 m (1 specimen); Stn 283, 61°07'30 N, 05°51'20 W, 284 m (2); Stn. 375, 61°10'04 N, 05°43'35 W 245 m (1); Stn 376, 61°09'51 N, 05°45'45 W, 250 m (1); Stn 378, 61°44'20 N, 05°42'35 W, 258 m (1) and to the north of the Faroes, Stn 352, 62°43'10 N, 07°22'40 W, 354 m (2).

Found in association with sponges, *Thenea levis* at Stn 377, and *T. valdiviae* at Stns 375, 376 and 378, hence the specific name. Sponge spicules were also with the specimen from Stn 27. The holotype is the largest complete specimen.

Very small species, body 7.5 by 0.8 mm with 34 segments of which 7 or 8 are thoracic; crown a further 5 mm, involuted ventrally at the base; 12 radioles on each side, each with small tapered tips, about six pairs of fine stylodes and no eyes; dorsal lips with tapered and grooved midribs, but no pinnular support, blunt tipped, and about one fifth length of crown; collar with wide gap dorsally and prominent paired ventral lappets; first segment similar in length to others in thorax; thoracic fascicles small, each with about 12 chaetae, these and those of abdomen like those of *B. moebii* (cf Figs 1g to k; 3g to j); thoracic uncinal crests more than half the length of the head, comprising about 20 fairly long and conspicuous teeth (Fig. 4 c, d); thoracic tori short (15 to 22 uncini in 5th and 6th tori) not reaching indistinct ventral shields (Fig. 3c); inter-ramal spots fairly large and very distinct, no other colouration.

As this species is found off Faroes, where the morphologically most similar *B. bahusiense* is also found, the possibility of it being a juvenile of the latter was considered. In *B. spongiarum*, however, the stylodes are relatively longer, compared with both breadth of stylode and width of radiole. *Branchiomma bahusiense* also differs in having 1) at least 5 times as many stylodes per radiole, 2) a crown base only 1/16 of crown length, compared with 1/6 in *B. spongiarum*, 3) thoracic uncini with a longer neck (cf. Figs 2s; 3f), and 4) uncinal crests smoother in profile (the small teeth lying closer to main fang) covering only half length of uncinal head (Fig. 4f). The blackish-red inter-ramal spots of *B. spongiarum* are very obvious against the pale body, whereas the minute inter-ramal spots of *B. bahusiense* are less noticeable against a background of pale pinkish-fawn. None of 19 Faroes specimens of *B. bahusiense* occurred at stations where *B. spongiarum* was found (although depths, 235-732 m, were similar) nor does *B. bahusiense* occur in association with sponges. It was commonly with *Sertella*.

Source : MNHN, Paris

*Branchionma infarctum*, *B. arcticum* and *B. moebii* differ from *B. spongiarum* in having larger bodies, wider more numerous stylodes, larger uncinal crests of relatively smaller teeth, and longer tori either approaching or

FIG. 2. — *Branchiomma infarctum* (Krøyer, a to d, j, k, m = holotype; f, g, h = Malmgren's, 1866, material): — a, whole animal lateral view. — b, detail of a. — c, ventral thorax. — d, dorsal thorax. — e, whole radiole and enlarged stylode (Kroyer's MS). — f, dorsal collar and base of crown. — g, dorsal basal stylodes from f. — h and j, thoracic uncini. — k, inferior thoracic chaeta. — m, ventral view of type before damage (Krøyer's MS). *B. bahusiense* Johansson, Faroes material: — n, dorsal thorax. — p, ventral thorax. — q, whole animal, inserts showing most of a dorsal radiole. — r, inferior thoracic chaeta. — s, thoracic uncinus. *B. arcticum* (Ditlevsen), Greenland material: — t, ventral thorax. — u, dorsal thorax. — v, whole animal. — w, lateral thorax (another specimen). — x, dorsal radiole. — y, thoracic uncinus. — z, inferior thoracic chaeta. Scales in mm: c, d, as b; j, s and y as h; n as p; w and u as t; z as k.

Source : MNHN, Paris

touching the ventral shields. *Branchiomma moebii* further differs in having shorter ventral collar lappets, very large inter-ramal spots, and a distinctive colour pattern. *Branchiomma inconspicuum* differs in having more numerous teeth on the uncinal crests.

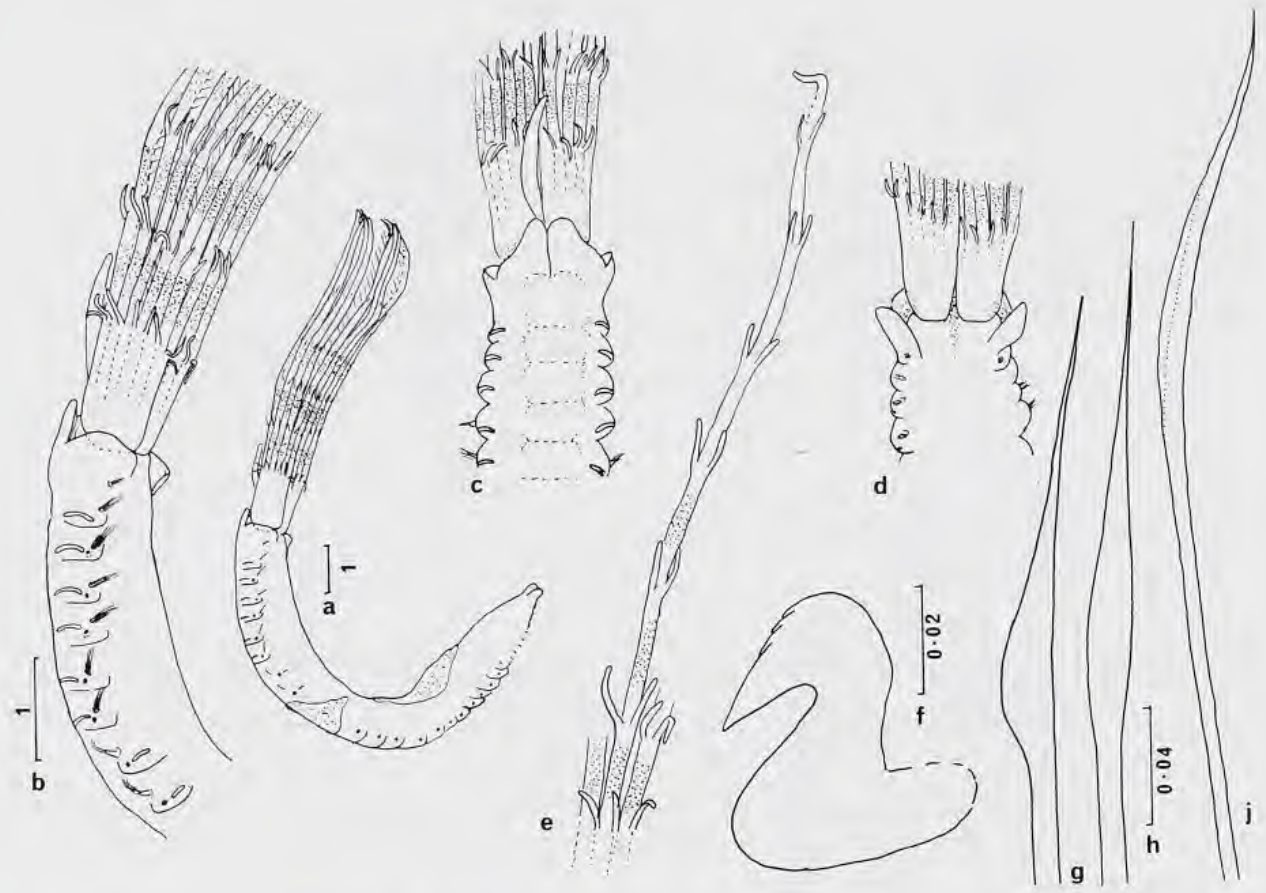



FIG. 3. — *Branchiomma spongiarum* sp. nov.: — a, Lateral view of holotype. — b, detail of a. — c, ventral thorax. —d, dorsal thorax. — e, dorsal radiole. — f, thoracic uncinus. — g and h, inferior thoracic chaetae, side and face view respectively. — j, superior thoracic chaeta. Scales in mm: c and d as b; g and j as h.

## STUDIES ON *PSEUDOBRANCHIOMMA* JONES AND *SABELLASTARTE* KRØYER

JONES (1962) suggested the genus *Pseudobranchiomma* for *P. emersoni*, a species like *Branchiomma* but with four thoracic segments and radioles with reduced stylodes and without eyes. FITZHUGH (1989) suggested three more characters separating *Pseudobranchiomma* from *Branchiomma*: radioles bearing flanges; dorsal lips without pinnular support; and abdominal fascicles with longer chaetae in the middle of the group. However, the latter character is also found in *Branchiomma*; presence or absence of pinnular support for a dorsal lip is rarely important (the holotype of *P. emersoni*, AMNH, has one of its lips free and the other attached to a pinnule); whilst possession of few thoracic segments is no more than a specific character, examples occurring in *Branchiomma* (e.g. *B. curta*) and other genera (e.g. *Perkinsiana* Knight-Jones, 1983). *Pseudobranchiomma* may thus seem closer to *Branchiomma* than envisaged by JONES (1962) and FITZHUGH (1989).

Source : MNHN, Paris

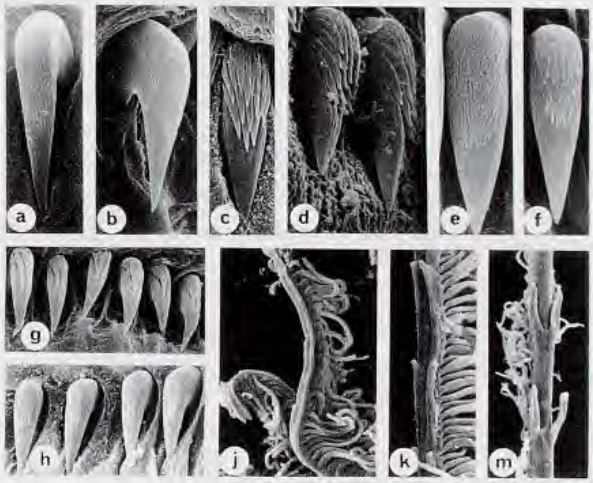



FIG. 4. — SEM of thoracic uncini (a to h) and radioles (j to m). — a and b, *Branchiomma moebii sp. nov.* — c and d, *B. spongiarum* sp. nov. — e, *B. arcticum* Ditlevsen. — f, *B. bahusiense* Johansson. — g, *B. cingulatum* (Grube). — h, *B. curtum* (Ehlers). — j, *Pseudobranchiomma emersoni* Jones from Cape Verde Islands (NHML). — k, *P. orientalis* (McIntosh) from Hong Kong (NMWC). — m, *Branchiomma moebii* sp. nov.

The so-called reduced stylodes of *Pseudobranchiomma*, however, are very different from *Branchiomma* stylodes, which are epithelial flaps arising more or less tranversely to the axis of the radiole (Fig. 4m). *Pseudobranchiomma* 'stylodes' are mere discontinuities in paired flanges along the radioles (Fig.4 j,k). Similar notched flanges are seen in *Sabella (Dasychone) serratibranchis* Grube, *Sabella tricolor* Grube, *Dasychone picta*, *D. orientalis* McIntosh, *D. kumari** Aziz, *D. odhneri* Fauvel and *Sabella zebuensis* McIntosh. These species should be included in *Pseudobranchiomma*, although some seem to be synonyms of others (study in progress). The notches in *odhneri* and *zebuensis*, however, are sparse and vestigial. Both species have been placed in *Sabellastarte* by DAY (1951) and HARTMAN (1959). DAY (1951) synonymised *odhneri* with *Sabellastarte longa* (Kinberg), but present studies show the two species to be distinct, yet similar enough to place *S. longa* in *Pseudobranchiomma* too, amending the only significant generic character to:- radioles with paired, longitudinal flanges, usually notched, but notches sometimes vestigial or absent. *Pseudobranchiomma odhneri* and *P. longa* both have eyes on the radioles so that character too should be amended to :- radioles with or without eyes. They, like the other species here placed in *Pseudobranchiomma*, have their dorsal collar margins free, not fused to the sides of the faecal groove.

There seems to be no type material of *Sabellastarte indica* (Savigny) (type species designated by HARTMAN, 1959), but species agreeing with SAVIGNY's definition (under "Tribu Sabellae Astarte") have a double row of [interdigitating] radioles, as in *Sabellastarte magnifica* (Shaw) and other species under study. These lack radiolar flanges (and eyes) and have dorsal collar margins fused to the midline groove. The latter character is not necessarily generic, for it varies within *Branchiomma* and both states (fused and free) can occur in a single species (*Megalomma heterops* PERKINS, 1984). Studies on *Pseudobranchiomma* and *Sabellastarte* are continuing so characters other than radiolar flanges may be found to separate these genera more conclusively. Like *Sabellastarte*, *Branchiomma* lacks such flanges.

Source : MNHN, Paris

## ACKNOWLEDGMENTS

I am much indebted for facilities, material and information to the directors and staffs of the following museums (shown in text above by initial letters): The American Museum of Natural History, New York (AMNH); the Natural History Museums of London (NHML), Paris (MNHNP), Stockholm (NRS) and Thorshavn (NHMT); the National Museum of Wales, Cardiff (NMWC) and the Zoological Museums of the Humboldt University, Berlin (ZMHUB) and of the Universities of Copenhagen (ZMUC), Oslo (ZMUO) and Uppsala (ZMUU). I am also very grateful to the Institute for Water Products Research, Bodrum, and the School of Biological Sciences, Swansea, for research facilities, and to Drs M.R. FORDY for help with SEM, Arne Nørrevang and Anne Klitgaard for material of *Branchiomma spongiarum* and information on associated sponges, Zeki ERGEN for help in collecting *B. moebii*, Mary E. PETERSEN for information about Kroyer's manuscript, Thomas H. PERKINS for valuable comments on this manuscript, the Systematics Association for a Wild microscope with drawing attachment, the Ray Society and Royal Society for travel grants and the Linnean Society of London (Appleyard Fund) for SEM costs.

## REFERENCES

BERTELSEN, E., 1937. — Contributions to the animal ecology of the fjords of Angmagssalik and Kangerdlugssuaq in East Greenland. *Meddr Grønland*, **108** : 1-58.

DAY, J., 1951. — The polychaete fauna of South Africa. Part 1. The intertidal and estuarine Polychaeta of Natal and Mozambique. *Annls Natal Mus.*, **12** : 1-67.

DITLEVSEN, H., 1937. — Polychaeta. The Godthaab Expedition 1928. *Meddr Grønland*, **80** : 1-64.

FITZHUGH, K., 1989. — A systematic revision of the Sabellidae - Caobangiidae - Sabellongidae complex (Annelida : Polychaeta). *Bull. Amer. Mus. nat. Hist.* **192** : 1-104.

HARTMAN, O., 1959. — Catalogue of the polychaetous annelids of the world. *Occ. Pap. Allan Hancock Fdn*, **23** : 1-628.

JOHANSSON, K.E., 1927. — Beiträge zur Kenntnis der Polychaeten-Familien Hermellidae, Sabellidae und Serpulidae. *Zool. Bidr. Upps.*, **11** : 1-184.

JONES, M.L., 1962. — On some polychaetous annelids from Jamaica, the West Indies. *Bull. Amer. Mus. Nat. Hist.*, **124** : 169-212.

KNIGHT-JONES, P., 1983. — Contributions to the taxonomy of Sabellidae (Polychaeta). *J. Linn. Soc. (Zool.)*, **79** : 245-295.

KNIGHT-JONES, P., 1992. — Sabellariidae and Sabellidae of the Faroes including some forgotten species. *In:* Marine Biology and Oceanography of the Faroe Islands (BIOFAR). A. NØRREVANG (ed).*Årbok 1991-92*. Nordurlandahusid i Føroyum, Torshavn, 100 pp.

KNIGHT-JONES, P. & FORDY, M. R., 1979. — Setal structure, functions and interrelationships in Spirorbidae (Polychaeta, Sedentaria). *Zool. Scr.*, **8** : 119-138.

KNIGHT-JONES, P., KNIGHT-JONES, E.W. & ERGEN, Z., 1991. — Sabelliform polychaetes mostly from Turkey's Aegean coast. *J. nat. Hist.*, **25** : 837-858.

LEVINSEN, G.M.R.,1886. — Kara-Havets Ledorme (Annulata). *In* : C.F. LUTKEN & J. HAGERUP (eds), Dijmphna-Togtets Zoologisk-botaniske Udbytte, København : 288-303

MALMGREN, A.J., 1866. — Nordiska Hafs-annulater. *Öfversigt. svenska Vetensk - Akad. Förh.*, **22** : 355-410.

PERKINS, Thomas H., 1984. — Revision of *Demonax* Kinberg, *Hypsicomus* Grube and *Notaulax* Tauber, with a review of *Megalomma* Johansson from Florida (Polychaeta: Sabellidae). *Proc. biol. Soc. Wash.*, **97** : 285-368.

SAINT-JOSEPH, A. de, 1906. — Les annélides Polychètes des côtes de France (Océan et côtes de Provence). *Annls Sci. nat. Paris*, sér. 9, **3** : 145-260.

Source : MNHN, Paris

# Redescription of *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830 (Polychaeta, Amphinomidae)

*Jerry D. KUDENOV*

Department of Biological Sciences
University of Alaska Anchorage
3211 Providence Drive
Anchorage, Alaska 99508 U.S.A.

ABSTRACT

The genus *Hipponoa* (Polychaeta, Amphinomidae) is monotypic. *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830, probably represents a highly specialized species whose affinities to amphinomids has been questioned. As part of an on-going study of Amphinomida, both the genus *Hipponoa* and species *H. gaudichaudi* are redescribed and emended. Affinities with other taxa of the order are briefly discussed.

RÉSUMÉ

**Redescription d'*Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830 (Polychaeta, Amphinomidae)**

Redescription de *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830 (Polychaeta, Amphinomidae). Le genre *Hipponoa* est monotypique. *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830, représente probablement une espèce très spécialisée dont les affinités avec les Amphinomidae sont discutées. Comme partie d'une étude en cours sur les Amphinomida, le genre *Hipponoa* et l'espèce *H. gaudichaudi* sont redécrits et émendés. Les affinités avec les autres taxa de l'ordre sont brièvement discutées.

## INTRODUCTION

On-going studies on the phylogenetic systematics of the polychaete Order Amphinomida (cf. KUDENOV, 1994) have revealed both historical questions and undescribed features for the amphinomid *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830. For example, MCINTOSH (1885) suggested that the setae of this species are not calcareous. This feature, coupled to the fact that *H. gaudichaudi* lacks a caruncle, led MCINTOSH and others to suspect that it was improperly assigned to the Amphinomidae. Indeed, the Order Amphinomida is highly diverged in the Class Polychaeta (DALES, 1962; CLARK, 1969). Removal of *Hipponoa* from the Amphinomidae may result in establishing another polychaete family (for which precedents exists, see CARUS, 1863; BAIRD, 1870). This decision cannot be made lightly. The purpose of this paper is to redescribe and emend the original of

KUDENOV, J.D., 1994. — Redescription of *Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830 (Polychaeta, Amphinomidae) in Polychaetes. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 199-207. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

*Hipponoa gaudichaudi*, and to address the question by McINTOSH and others about the affinity of this species with the Amphinomidae.

## MATERIALS AND METHODS

Materials of *Hipponoa gaudichaudi* were obtained both from the Smithsonian Institution (USNM) and the Allan Hancock Foundation Polychaete collection of the Los Angeles County Museum of Natural History (LACM-AHF). Tissue sections were made following specifications noted by KUDENOV (1977). Preliminary SEM work was performed at the USNM on preserved specimens held in the general collection.

Family Amphinomidae Lamarck, 1818
Genus ***Hipponoa*** Audouin & Milne-Edwards, 1830, emended

*Hipponoa* AUDOUIN & MILNE-EDWARDS, 1830: 156. — CUVIER, 1831: 18; MILNE-EDWARDS, 1838: 464. — COSTA, 1841: 270. — FAUCHALD, 1977: 102.

*Hipponoe* CARUS, 1863: 28. — QUATREFAGES, 1865: 409-410. — TREADWELL, 1939: 177. — GARDINER, 1975: 103. — *Non* TREADWELL, 1931: 3-4, figs. 10-12.

*Hipponoë* AUDOUIN & MILNE-EDWARDS, 1834: 116. — HOEVEN, 1850-1856: 244. — GRUBE, 1850: 289. — SCHMARDA, 1861: 134. —BAIRD, 1870: 239-240. — FAUVEL, 1913: 32; 1923: 132. — HORST, 1886: 170. — AMOUREUX, 1972: 51.

*Hypponnë* AUDOUIN & MILNE-EDWARDS, 1834: 117.

*Metamphinome* TREADWELL, 1940: 1.

**Emended Diagnosis.** — Body of adult fusiform, dorsoventrally flattened, with up to 105 setigers. Prostomium with five antennae, two pairs of eyes. Caruncle absent. Nuchal organ present. Mouth ventral. Notopodia on laterum. Neuropodia on ventrum. Dorsal cirri numbering one per notopodium. Ventral cirri papilliform. Notosetae all capillaries. Neurosetae retractile, hooks generally bidentate; may be unidentate. Branchiae planar, bipinnate. Anus terminal.

**Remarks.** — This emended diagnosis differs from those presented previously in that a nuchal organ is present, branchiae are planar and bipinnate, and the anus is terminal. Neurosetal hooks are generally bidentate in specimens with around 30 or fewer segments, and unidentate in a single specimen with 105 segments.

***Hipponoa gaudichaudi*** Audouin & Milne-Edwards, 1830, emended
Figs 1-2

*Hipponoa gaudichaudi* Audouin & Milne-Edwards, 1830: 156-159, Pl. III, fig. 4-4a-4b. — AUDOUIN & MILNE-EDWARDS, 1834: 128-129, Pl. II, fig. 10-10 bis. — GUÉRIN, 1829-1843: 1-14, Pl. IV, fig. 3, 3A-3D — CUVIER, 1831 : 19. — IBAÑEZ, 1973: 124.

*Hipponoa gaudichaudi agulhana* DAY, 1967: 122, fig. 3.1 a-e.

*Hipponoa gaudichaudii* CUVIER, 1831: 18. — MILNE-EDWARDS, 1838: 464.

*Hipponoe gaudichaudi* BAIRD, 1870: 239-240. —McINTOSH, 1885: 30-33, Pl. I, fig. 5, Pl. IV, fig. 3, Pl. IIIA, figs. 13-17. —HORST, 1886: 170-171. — FAUVEL, 1913: 32; 1914: 89, Pl. I, fig. 2, 12; 1923: 132, Fig. 47 l-p; 1936: 19. — PETTIBONE, 1963: 57-59, fig 13 a-b. — FAUVEL & RULLIER, 1959: 510. — AMOUREUX, 1972 : 51.

*Hipponoe gaudichaudi* HOEVEN, 1850-56: 244. —GRUBE, 1850: 289.

*Hipponoe Gaudichaudi* STOP-BÖWITZ, 1948: 15.

*Hipponoe Gaudichaudi* CUVIER, 1830: 199. —MILNE-EDWARDS, 1836: 31-32, Pl VIII, fig 4, 4a,b. — CARUS, 1863: 28. — QUATREFAGES, 1865: 410. — MOORE, 1903: 793. — WILLEY, 1910: 180. — SUMNER, OSBURN & COLE, 1913: 619. — AUGENER, 1922: 39. — OKUDA, 1950: 49, figs a-b.— GARDINER, 1975 : 103, fig. 5 l-m.

*Hipponoe gaudichaudi gigantea* Hartmann-Schröder, 1981: 24-25, figs. 1, 2.

*Hipponoe multibranchiata* Hartman 1951: 29, Pl. 8, figs. 1-2.

Non *Metamphinome multibranchiata* Treadwell, 1940: 1-2, figs. 1-3.

*Hipponoe cranchii* Baird, 1870: 240, Pl. VI, figs. 7-14.

Non *Hipponoe elongata* Treadwell, 1931: 3-4, fig. 10-12; 1939: 177-178, Fig. 11.

Source : MNHN, Paris

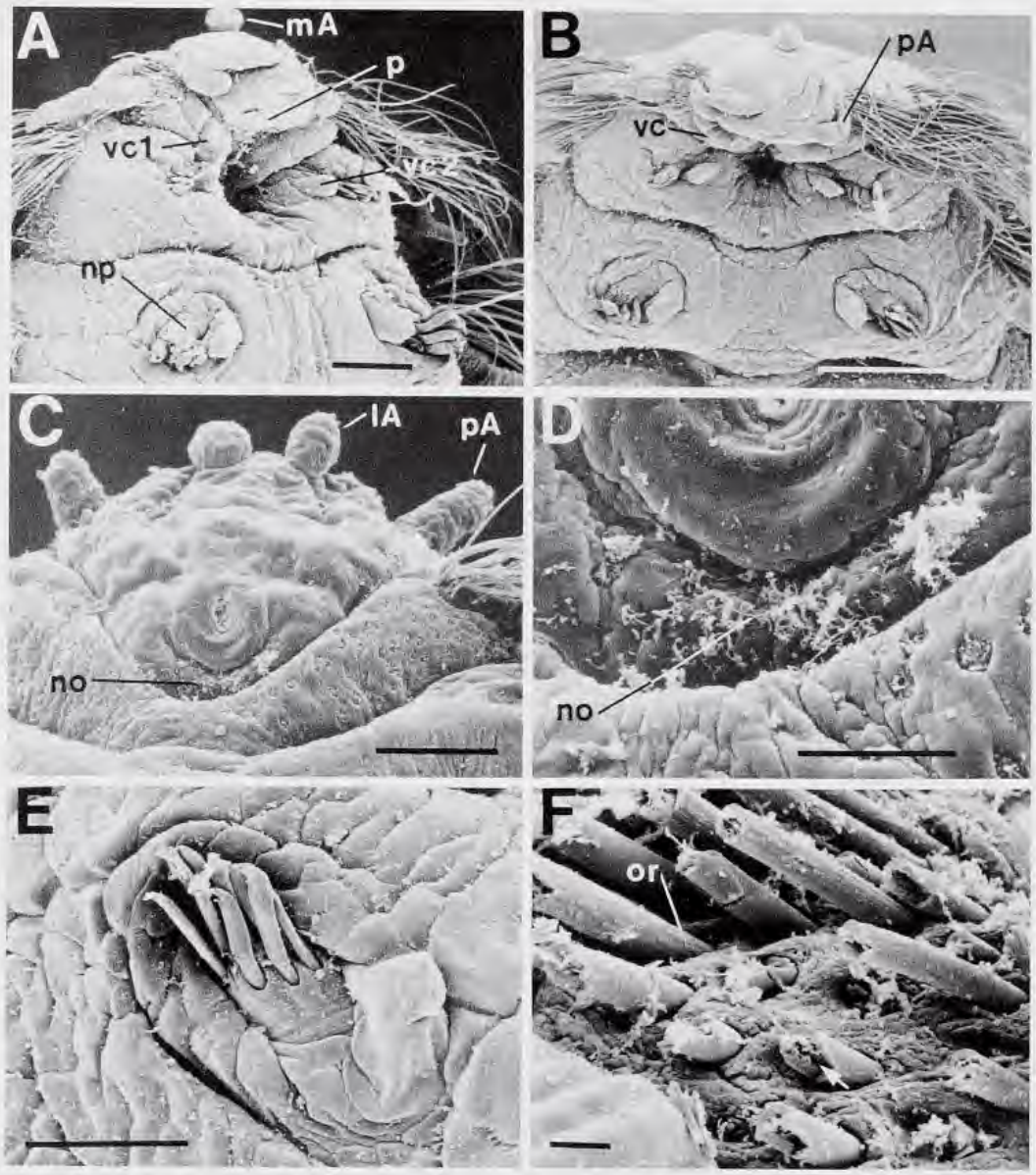



FIG. 1. — *Hipponoa gaudichaudi* Audouin & Milne-Edwards : A, prostomium and anterior segments of adult, ventrolateral view. —B, same, anteroventral view. —C, same of juvenile lacking median antenna, dorsal view. —D, same, detail of nuchal organ, dorsal view. —E, neuropodium, ventral view. —F, sheared capillary notofascicle revealing hollow core (arrow). Abbreviations: lA, lateral antenna; mA, median antenna; no, nuchal organ; np, neuropodium; or, notosetal ornamentation; p, palps; pA, palpal antenna; vc, ventral cirrus; vc 1, padlike ventral cirrus of setiger 1; vc 2, ventral cirrus of setiger 2. Scales : A = 0.2 mm; B = 0.4 mm; C = 0.1 mm; D = 20 µm; E = 0.2 mm; F = 10 µm.

Source : MNHN, Paris

**Material examined**. — North Atlantic Ocean, Gulf Stream, Surface, R/V *Albatross*, coll. J.E. BENEDICT, 20 specimens (USNM 16311) ; 3 specimens (USNM 32374). — Bermuda, south shore, 5 Aug 1948, coll. H. Ris, three specimens (LACM-AHF, n5858 from HARTMAN ledger).

Caribbean Ocean, Panama, Galeta Point, 14 Jul 1976, in sargassum rafts washed onto reef flats, coll. G. HENDLER, 1 specimen (USNM 58724). — Louisiana, Grand Isle, coll. H. BENNETT, 4 (LACM-AHF, n10183 from HARTMAN ledger).

North Pacific Ocean, 30°50'N, 121°35'W, 29 May 1954, in *Lepas fascicularis* Ellis & Solander, coll. D. HENRY, 19 specimens (USNM 32366); 27°56'N, 119°36'W, 23 Apr 1954, in *L. anatifera* Linnaeus, two specimens (USNM 32367); 27°56'N, 119°36'W, 23 Apr 1954, in *L. fascicularis* Ellis & Solander, six specimens (USNM 32368); 28°40'N, 129°35'W, Jun 1955, in *L. anatifera* Linnaeus, two specimens (USNM 32369); 30° N, 118° W, 4 May 1954, one specimen (USNM 32370); 26°12'30" N, 118°27' W, 24 Aug 1954, in *L. fascicularis* Ellis & Solander, two specimens (USNM 32371); 30° 50'N, 121°35'W, 29 May 1954, in *L. pectinata* Spengle, one specimen (USNM 32372); 27°56'N, 119°36'W, 23 Apr 1954, in *L. anatifera* Linnaeus, 5 specimens (USNM 32373); Off Japan, 28°02'N, 155°58'E, 29 Apr 1970, coll. G. CHASE, 2 specimens (USNM 43205). —?Pacific Ocean, 9 Jun 1961, coll. D. DAVENPORT, seven adults + numerous juveniles (LACM-AHF).

**Description**. — Body of adults fusiform, dorsoventrally flattened, 24-105 mm long, 5-18 mm wide without setae, totalling 20-46 setigers; dorsum broadly exposed. Color in life bright orange.

Prostomium a small, single, rhomboid-shaped lobe, with 5 cirriform antennae (Fig. 1c-d). Median antenna about as long as prostomium, lacking ceratophore (Fig. 2a). Lateral antennae arising from frontal, dorsomedial surface, about 0.6 times length of median antenna (Fig. 2a). Palpal antennae arising from anterolateral surfaces of palps, somewhat more stout and shorter than lateral antennae (Figs 1a-b; 2b). Eyes numbering two pairs, located anterior to median antenna, where prostomium is widest, all small, inconspicuous. Caruncle absent. Nuchal organ present as ciliated patch on posterior prostomium, best observed in specimens with fewer than 15-18 setigers (Figs 1c-d; 2a). Palps fused into single lobe, forming upper lip of mouth and short midventral groove (Figs 1a-b; 2b). Mouth ventral, opening between setigers 1-2; setigers 1-2 forming lateral lips of mouth; setiger 2 posterior lip (Figs 1a-b; 2b).

Setiger 1 with setigerous notopodia, neurosetae absent, neuropodia only represented by pad-shaped ventral cirri (Figs 1a-b; 2b). Parapodia biramous, setigerous from setiger 2 to end of body; rami more widely separated from one another compared to setiger 1. Notopodia as transverse ellipses in outline in dorsal view, confined to extreme dorsolaterum; notopodial lobes not raised above general body surface. Neuropodia circular to slight transverse ellipses in outline in ventral view, confined to ventrum (Fig. 1e); neuropodial lobes resembling retractable papillae surrounded by thick, glandular collars of tissue (Fig. 1e) with papilliform ventral cirri.

Parapodial cirri present on all setigers. Dorsal cirri cirriform, with basal cirrophore two times longer than wide, distal style about 2-3 times longer than cirrophore; arising from body wall behind inferior notosetal fascicle margin, not within notosetal fascicle. Ventral cirri papilliform, lacking basal cirrophores, slightly longer than wide; arising medially from collar of neuropodium that encircles neurosetal fascicles (Figs 1a-b, e; 2b).

Notosetal fascicles with numerous setae directed laterally in all setigers. Notosetae hollow (Fig. 1f, arrow), slender capillaries with file-like teeth on shafts (Fig. 1a-b, f), calcareous, accessory subdistal spurs absent, tapering distally to fine, entire tips (Fig. 1a-b). Neurosetae from setiger 2 of one kind; chitinous, solid, distally bidentate hooks with longitudinal striae, numbering around 10 per fascicle (Fig. 1e). Notoaciculae inconspicuous, capilliariform, numbering 3-5 per fascicle, limited to posterior notopodial margin. Neuroaciculae from setiger 2 distally curved, distally embedded in clear cuticular matrix, non-emergent, numbering 8 per fascicle, in single, long, dorsal rows along superior or outer lateral margins of neuropodia (Fig. 2c).

Branchiae bipinnate, pinnae branching alternately off primary branchial axis, each pinna in turn branching up to 6 times basally and having fewer branches distally (Fig. 2d-e); pattern more conspicuous in small specimens. Branchiae present from setiger 3 to end of body, numbering 1 pair per segment, tending to be planar, particularly in small specimens (Fig. 2d) than in larger ones (Fig. 2e). Branchial bases broad, arising posterodorsally to dorsal cirri, not extending beyond notosetae. Branchiae gradually increasing in length and development to midbody, gradually becoming shorter, less developed to end.

Pygidium with terminal anal cirrus; anus opening through anal cirrus (Fig. 2f).

**Distribution**. — Cosmopolitan in tropical and warm temperate oceans.

**Remarks**. — *Hipponoa gaudichaudi* has been reported from numerous localities throughout the world, and its description has not significantly changed since AUDOUIN & MILNE-EDWARDS (1830) first described and BAIRD (1870) later emended it. As presently understood, *H. gaudichaudi* appears to be a highly modified and specialized member of the Amphinomidae, probably reflecting the fact that it is an inquiline of barnacles (*Lepas* species;

Source : MNHN, Paris

BAIRD, 1870; AUGENER, 1910; KUDENOV, 1977). Although *H. gaudichaudi* retains many features of the Amphinomida, it is generally quite unlike most amphinomids (GUSTAFSON, 1930 ; KUDENOV, 1994).

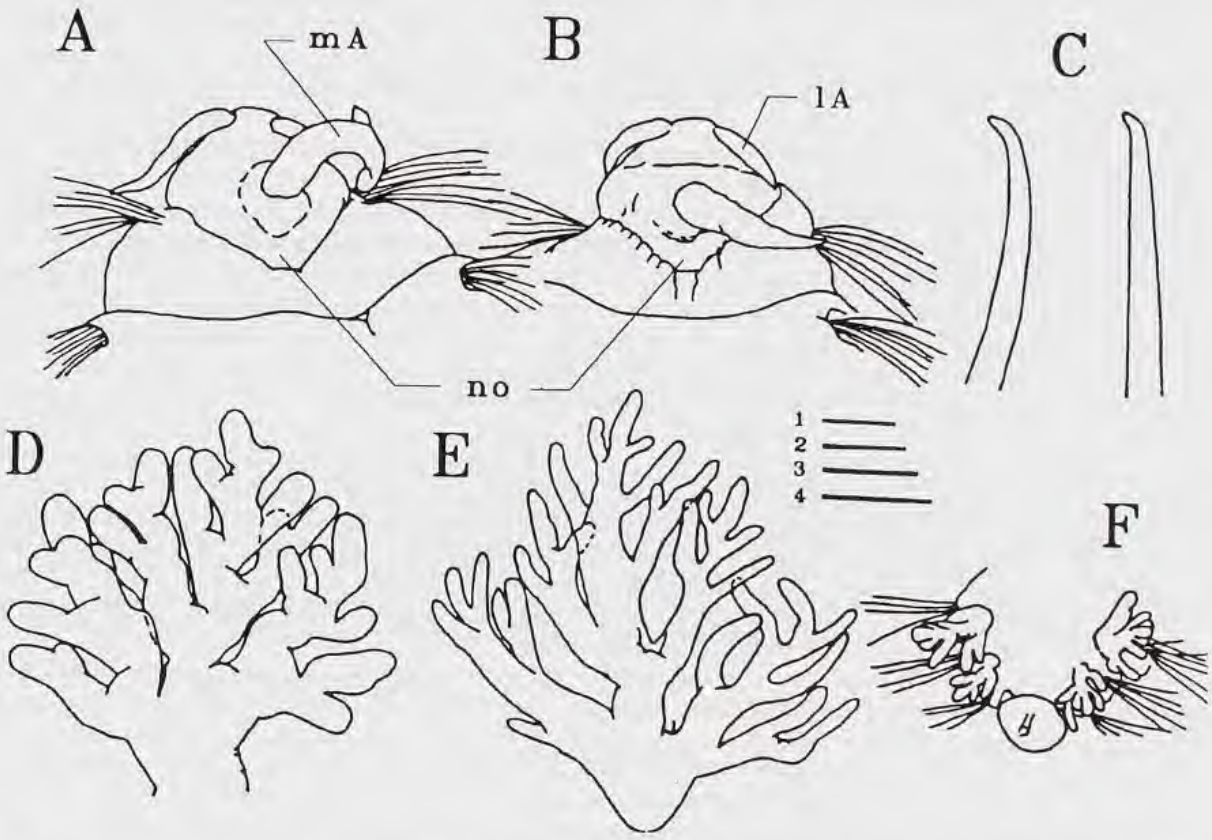



FIG. 2. — *Hipponoa gaudichaudi* Audouin & Milne-Edwards: A — B, Prostomium showing only three of five antennae and setiger 1, dorsal view. — C, neuroaciculae. — D, bipinnate branchia from right setiger 10, anterior view. — E, same, from left setiger 13, anterior view. — F, pygidium, dorsal view. Abbreviations : see legend for Fig. 1. Scales : 1 = 0.25 mm, F; 2 = 10 µm, D; 3 = 30 µm, E and 5 µm, C; 4 = 0.2 mm, A, B.

For example, *H. gaudichaudi* differs from the general amphinomid pattern in that its body is strongly flattened and fusiform, and is the only known genus with a continuous midventral groove. Its prostomium is strongly reduced to a single lobe with palpal antennae arising from the anterolateral margins of the prostomium. Palps are extremely short, narrow, and fused medially, and are confined to the ventral area lying between the mouth and prostomium (Fig. 2b; KUDENOV, 1993). The mouth is present very close to the prostomium at the junction of setigers 1-2 (Fig. 2b). Setiger 1 is dorsally complete, and is not interrupted by a caruncle. Notopodia arise from the extreme dorsolaterum; neuropodia from the ventrum. The notosetae are entirely nonspurred capillaries; it is the only presently known genus of the family in which the notosetae are represented solely by capillaries. The dorsal cirri arise directly from the body wall as they do in the Euphrosinidae, and not from within the notopodial field as is typical of Amphinomidae. Obviously, *H. gaudichaudi* is quite unlike the Amphinomidae sensu lato in many of its features.

Additional traits either confirmed or newly discovered as part of this study can be added to this list. *H. gaudichaudi* is characterized by the: 1) lack of a caruncle; 2) a poorly ciliated, mound-shaped nuchal organ; 3) absence of both neuropodia and neurosetae in setiger 1; 4) reduced dorsal cirri in setiger 1; 5) lack of cirriphores on ventral cirri; 6) hollow calcareous notosetae; 7) solid neurosetae that may be chitinous; 8) planar, bipinnate branchiae; and 9) a terminal anus opening through an anal cirrus. All except the first and third of these traits are newly reported.

The nuchal organ is poorly ciliated, and more conspicuous as a mound-shaped lobe on the posterior prostomium in juveniles and subadults than in larger individuals, such as functionally mature females. This finding

Source : MNHN, Paris

may be expected, given the fact that *H. gaudichaudi* is a protandric hermaphrodite (KUDENOV, 1977). It is hypothesized that immature individuals rely on nuchal organs and chemical senses to a much greater extent compared to mature worms to maintain body contact with their brooder, to obtain food, and to subsequently locate other barnacles. The nuchal organ must therefore be relatively better developed in immature individuals.

The lack of neuropodia and neurosetae in setiger 1 was previously noted by DAY (1967) who made no further comments about its significance. In this specialized amphinomid, setiger 1 is strongly modified and forms the lateral margins of the mouth. It is so small that most light microscopical observations of this segment have lead workers to assume the presence of neuropodia and neurosetae. The ventral cirri of setiger 1, which are both reduced and very close to the mouth, may function in feeding. Moreover, *H. gaudichaudi* is the only described amphinomid species in which ventral cirri lack cirriphores.

McINTOSH (1885) particularly, and other workers generally, questioned whether the setae of *H. gaudichaudi* are calcareous as those of other amphinomids. He strongly suggested that *H. gaudichaudi* is not typical of other amphinomids whose setae produce gas bubbles when they are treated with weak acetic acid. McINTOSH conveys the impression that he would have assigned *Hipponoa* to another taxon if he had had additional evidence. Both CARUS (1863) and BAIRD (1870) had previously proposed the Hipponacea and Hipponoidae, respectively. SEM studies revealed notosetal ornamentation (Fig. 1f) usually associated with the calcareous setae of the Amphinomida (KUDENOV, 1993, 1994). Tissue sections through notosetal fascicles tend to splinter the setae of non-decalcified specimens, leaving fragments of a clear outer layer assumed to be calcareous (KUDENOV, unpublished). *H. gaudichaudi* is clearly related to the Amphinomidae also by the fact that its notosetae are hollow (Fig. 1f), a feature shared by all other members of the order (KUDENOV, 1994). However, its neurosetal hooks may not be calcareous. All appear solid in both SEM and tissue section preparations, lack ornamentation referred to above, and have densely packed longitudinal striae reminiscent of chitinous setae. Confirmation of these observations awaits the receipt of fresh specimens. These setal data are presently insufficient to define relationships between *Hipponoa* and other Amphinomida; they will eventually be refined and included in a cladistic evaluation of the order Amphinomida (KUDENOV, 1994).

The branchiae of *H. gaudichaudi* have generally been described as being tuft-like, arborescent or dendritically branched and bushy. All such terms are misleading. In fact, the branchiae are all bipinnate and planar (Fig. 2d-e), a condition most obvious in juveniles which is clearly retained in adults, and reminiscent of those found in the *Chloeia* species complex. However, primary branchial axes in *Hipponoa gaudichaudi* may be contractile; degrees of contraction ranging from a long, slender zig-zagging to a stout, basal axis sometimes obscuring the bipinnate pattern. Both taxa also have lateral cirri (mistaken for true dorsal cirri which are present in setigers 1-4 of *Chloeia*) arising directly from the body wall and outside the notopodial field. No attempt to imply common ancestry between these taxa is intended.

Another overlooked character in *H. gaudichaudi* is the presence of a terminal anus that opens through the anal cirrus (the presence of a dorsal anus has been assumed [e.g., FAUVEL, 1923]). In other members of the Amphinomidae, the anus opens on the dorsum of the last few body segments, above an associated, unpaired anal papilla. The anus of Euphrosinidae is terminal, and opens between or above paired anal cirri (KUDENOV, 1994). The unusual anus of *H. gaudichaudi* presumably reflects its highly specialized life style, enabling it to void its feces without fouling either itself or its host. This point can only be answered by studying live specimens of both the worm and its host.

The synonymies listed above are not intended to be exhaustive. Analysis of the earliest literature shows AUDOUIN & MILNE-EDWARDS (1830) original record from Port Jackson, Australia, was quoted by subsequent workers. BAIRD (1870) published what appears to be the second record of the species from the eastern equatorial Atlantic and Madeira. He described a second species, *H. cranchii*, which his illustrations show to be a juvenile *Amphinome* (?*rostrata*), and not a second species of *Hipponoa*. The third record of *H. gaudichaudi* was from the *Challenger* expedition, and McINTOSH (1885) provided extensive observations about it, including the presence of capillary notosetae having distally forked ends. Such notosetae have not been reported for *H. gaudichaudi* at any other time prior or subsequent to his work. HORST (1886) represents the fourth record, after which time the species was more commonly encountered. DAY (1967, Fig. 3.1.a-e) later described the subspecies, *H. gaudichaudi agulhana*, based on the absence of notosetae as described by McINTOSH (1885). It is suggested that McINTOSH observed frayed or damaged notosetae that appeared distally forked. Another, *H. gaudichaudi gigantea* Hartmann-Schröder (1981) was distinguished on the basis of body size and hook morphology. Although the specimens she examined were up to 105 mm long, neurosetal hook morphology may reflect size-dependent relationships instead of polyploidy, as implied by HARTMANN-SCHRÖDER. Moreover, distinction between the terms "Normalform" and

Source : MNHN, Paris

"Riesenform" used by HARTMANN-SCHRÖDER to describe *H. gaudichaudi gigantea* are typological, and seem to preclude a continuum of morphological change associated with allometric growth.

The genus *Hipponoa* supposedly represents three described species (FAUCHALD, 1977) including *H. gaudichaudi*, *H. cranchii* Baird, 1870, and *H. elongata* Treadwell, 1931. *Metamphinome multibranchiata* Treadwell, 1940 was referred to *Hipponoa* by HARTMAN (1951) and *H. gaudichaudi* by PETTIBONE (1963). All previous descriptions and illustrations are sufficiently clear to indicate *H. cranchii* is probably a juvenile *Amphinome*, and *H. elongata* is most certainly a *Linopherus*-like species. Therefore, the genus *Hipponoa* is presently monotypic.

In summary, the species description of *Hipponoa gaudichaudi* is emended with certain observations confirmed and additional characters newly reported. The species seems to be highly specialized and derived; departs substantially from the general features normally attributed to the Amphinomidae (KUDENOV, 1994); and seems to be cosmopolitan in tropical, subtropical and warm-temperate oceans. But is this taxon truly cosmopolitan and monotypic? Only a thorough systematic study involving specimens from various points throughout its range can answer these and other questions.

## ACKNOWLEDGEMENTS

I am indebted to Kristian FAUCHALD, Greg ROUSE and Linda WARD, all from the National Museum of Natural History, and Len HIRSCH, Office of International Relations, Smithsonian Institution, Washington D.C., for their assistance, support, encouragement and insights offered throughout this study. I especially thank Greg ROUSE for his assistance with the SEM. I also thank Kirk FITZHUGH and Leslie HARRIS, Los Angeles County Museum of Natural History, for loan of materials and for verifying literature citations. Editorial comments made by Kirk FITZHUGH and an anonymous reviewer improved this paper. Debra LACHINSKI provided the initial version of the abstract in French.

## REFERENCES

AMOUREUX, L. 1972. — Annélides polychètes du Maroc. *Bull. Soc. Sci. nat. phys. Maroc*, **52** : 47-72.

AUDOUIN, J.V. & MILNE-EDWARDS, H. 1830. — Description de l'*Hipponoe*, nouveau genre d'Annélides. *Annls. Sci. Nat.* **20** : 156-159.

AUDOUIN, J.V. & MILNE-EDWARDS, H. 1834. — *Recherches pour servir à l'histoire naturelle du littoral de la France, 2 Annélides*. Paris, 290 pp.

AUGENER, H. 1910. — Bemerkungen über einige Polychaeten von Roscoff, über zwei neue Polynoiden des Berliner Museums und über die Bruthflege von *Hipponoe gaudichaudi* Audouin & Milne-Edwards. *Zool. Anz.*, **36** : 232-249.

AUGENER, H. 1922. — Über litorale Polychaeten von Westindien. *Sber. Ges. naturf. Freude, Berl.*, 1922 : 38-53.

BAIRD, W. 1870. — Contribution towards a monograph of the species of annelids belonging to the Amphinomacea with a list of the known species and a description of several new species belonging to the group contained in the national collection of the Bristish Museum, to which is appended a short account of two hitherto nondescript annulose animals of larval character. *J. Linn. Soc. Zool.*, **10** : 215-246.

CARUS, J.V. 1863. — Class Annulata. *In* : J.V. CARUS, W.C.H. PETERS & E.A. GERSTAECHER (eds), *Handbuch der Zoologie*. 642 pp.

CLARK, R.B. 1969. — Systematics and Phylogeny : Annelida, Echiura, Sipunculida. *In*: M. FLORKIN & B.T. SCHEER (eds), *Chem. Zool.*, **4** : 1-68.

COSTA, O.G. 1841. — Description des quelques annélides nouvelles du Golfe de Naples. *Ann. Sci. natur. Zool. France, (2)*, **16** : 267-280.

CUVIER, B.G. 1830. — *Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et l'introduction à l'anatomie comparée*. Nouvelle Edition, Revue et Augmentée, Paris, **3** : 186-217.

CUVIER, B.G. 1831. — *The Animal Kingdom. Arranged in conformity with its organization, by the Baron Cuvier*. Translated from the French, with notes and additions by H.M. MURTRIE, M.D. New York, **2,** 475 pp.

Source : MNHN, Paris

DALES, R.P. 1962. — The polychaete stomodaeum and the interrelationships of the families of Polychaeta. *Proc. Zool. Soc. Lond.*, **139** : 398-428.

DAY, J.H. 1967. — A Monograph on the Polychaeta of South Africa. Part I. Errantia. *Trust. Brit. Mus. (Nat. Hist.)*, London **656** : 1-458.

FAUCHALD, K. 1977. — The Polychaete Worms. Definitions and Keys to the Orders, Families and Genera. *Natural History Museum of Los Angeles County, Science Series*, **28** : 1-190.

FAUVEL, P. 1913. — Quatrième note préliminaire sur les polychètes provenant des campagnes de l'*Hirondelle* et de la *Princesse Alice* ou déposées dans le Museé Océanographique de Monaco. *Bull. Inst. océanogr., Monaco*, **27** : 1-80.

FAUVEL, P. 1914. — Annélides polychètes non-pélagiques provenant des campagnes de l'*Hirondelle* et de la *Princesse Alice* (1885-1910). *Résult. Camp. Scient. Prince Albert I*, **46** : 1-432.

FAUVEL, P. 1923. — Polychètes errantes. *Faune Fr.*, **5** : 1-488.

FAUVEL, P. 1936. — Contribution à la faune des Annélides polychètes du Maroc. *Mém. Soc. Sci. nat. phys. Maroc*, **43** : 1-143.

FAUVEL, P. & F. RULLIER. 1959. — Contribution à la faune des Annélides Polychètes du Sénégal et de Mauritanie. *Bull. Inst. Français Afrique Noire, sér A*, **21** : 477-533.

GARDINER, S.L. 1975. — Errant polychaete annelids from North Carolina. *J. Elisha Mitchell Sci. Soc.*, **91** : 78-200.

GRUBE, A.E. 1850. — Die Familien der Anneliden. *Arch. Naturgesch.*, **16** : 249-364.

GUÉRIN, M.F.E. 1829-1843. — *Iconographie Règne Animal de G. Cuvier*. Paris. Part 1 : 1-14.

GUSTAFSON, G. 1930. — Anatomische Studien über die Polychäten-Familien Amphinomidae und Euphrosynidae. *Zool. Bidr. Upps.*, **12** : 305-471.

HARTMAN, O. 1951. — The littoral marine annelids of the Gulf of Mexico. *Publ. Inst. mar. Sci. Univ. Tex.*, **2** : 7-124.

HARTMANN-SCHRÖDER, G. 1981. — Die Polychaeten der Fahrten 11, 19, 21 und 26 (1967-1972) von F.S. "Meteor" in das Gebiet zwischen dem Golf von Biscaya und dem Auftriebsgebiet vor Westafrika. *"Meteor" Forsch.-Ergebnisse D*, **33** : 23-36.

HOEVEN, J. VAN DER. 1850-1856. — Class Annulata. *Handbuch der Zoologie*. [Translated into English from the Dutch]. Cambridge University Press, London, **1** : 219-246.

HORST, R., 1886. — Contributions towards the knowledge of the Annelida Polychaeta. Pt. I. Amphinomidae. *Notes Leyden Mus.*, **8** : 157-184.

IBAÑEZ, M. 1973. — Catalogo de los anelidos polyquetos citados en las costas españolas. *Cuad. C. Biol.*, **2** : 121-140.

KUDENOV, J.D. 1977. — Brooding behavior and protantry in *Hipponoe gaudichaudi* (Polychaeta: Amphinomidae). *Bull. So. Calif. Acad. Sci.*, **76** : 85-90.

KUDENOV, J.D. 1993. — Amphinomidae and Euphrosinidae (Annelida: Polychaeta) principally from Antarctica, the southern ocean and subantarctic regions. *Biol. Antarct. Seas XXII, Antarct. Res. Ser.*, **58** : 93-150.

KUDENOV, J.D. 1994. — The Order Amphinomida : A revision of the families (Annelida: Polychaeta). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. Natin. Hist. nat.*, **162** : 625.

LAMARCK, J.B. de, 1818. — *Histoire naturelle des Animaux sans vertèbres ou tableau général de classes, des ordres et des genres de ces animaux présentant leur caractères essentiels et leur distribution, d'après la considération de leur rapports naturelles et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Histoire Naturelle, parmi leurs dépouilles conservées; précédé du discours d'ouverture du cours de zoologie, donné dans le Muséum National d'Histoire Naturelle l'an 8 de la République*. Paris, V. 612 pp.

MCINTOSH, W.C. 1885. — Report on the Annelida Polychaeta collected by the H.M.S. *Challenger* during the years 1873-1876. *Rep. Scient. Results Challenger (Zool.)*, **12** : 1-554.

MILNE-EDWARDS, H. 1836. — Les Annélides. *In* : Cuvier, G (éd.), *Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux, et l'introduction à l'anatomie comparée*. Paris, **15-16** : 31-32.

MILNE-EDWARDS, H. 1838. — Les Annélides. *In* : Cuvier, G. (éd.), *Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux, et l'introduction à l'anatomie comparée*. Paris, **9** : 464.

MOORE, J.P. 1903. — Some pelagic Polychaeta new to the Woods Hole fauna. *Proc. Acad. nat. Sci. Phila.*, **55** : 720-726.

Source : MNHN, Paris

OKUDA, S. 1950. — Notes on some commensal polychaetes from Japan. *Annot. Zool. Japon.*, **24** : 49-53.

PETTIBONE, M.H. 1963. — Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. *Bull. U.S. natn. Mus.*, **227** : 1-346.

QUATREFAGES, A. de, 1865. — *Histoire naturelle des Annelés marins et d'eau douce. Annélides et Géphyriens.* Librairie Encyclopédique de Roret, Paris, **1**, 588 pp.

SCHMARDA, L.K. 1861. — *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. I. Turbellarien, Rotatorien und Anneliden.* Leipzig, 164 pp.

STÖP-BOWITZ, C. 1948. — Polychaeta from the *Michael Sars* North Atlantic deep-sea expedition 1910. *Rep. scient. Results Michael Sars N. Atlant. deep-sea Exped.*, **5** : 1-91.

SUMNER, F.B., R.C. OSBURN & L.J. COLE. 1913. — Annulata. *In*: A biological survey of the waters of the Woods Hole and vicinity. *Bull. U.S. Bur. Fish.*, **31** : 615-636.

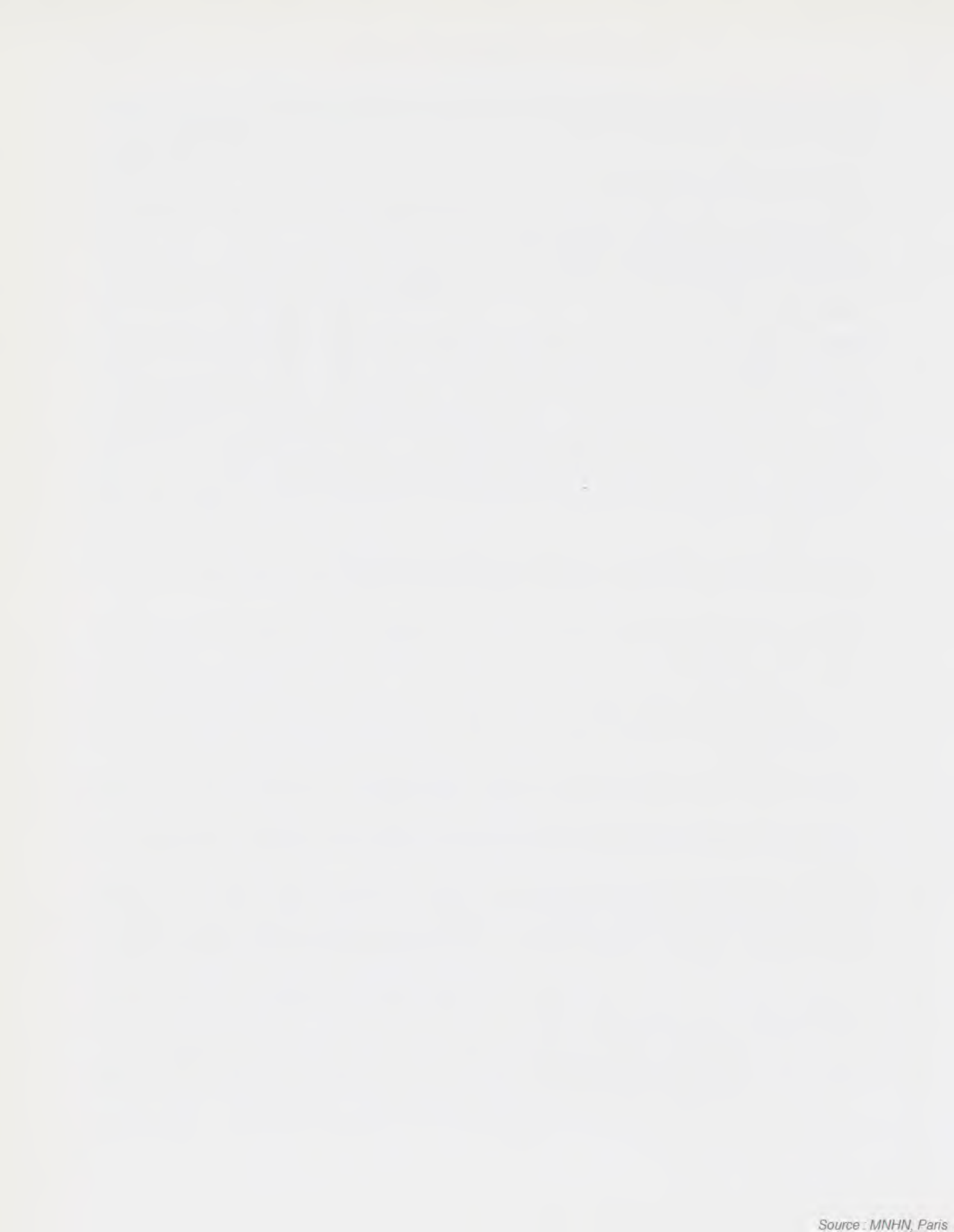
TREADWELL, A.L. 1931. — New species of polychaetous annelids from California, Mexico, Porto Rico, and Jamaica. *Amer. Mus. Novitat.*, **484** : 1-13.

TREADWELL, A.L. 1939. — Polychaetous annelids of Porto Rico and vicinity. Scientific Survey of Porto Rico and the Virgin Islands. *Acad. Sci. New York*, **16** : 151-319.

TREADWELL, A.L. 1940. — A new genus and two new species of polychaetous annelids from Texas and one new species from the Philippines Islands. *Amer. Mus. Novit.*, **1089** : 1-4.

WILLEY, A. 1910. — Association of barnacles with snakes and worms. *Spolia Zeylanica*, **6** :180-181.

Source : MNHN, Paris



Source : MNHN, Paris

# Sabellariidae (Annelida, Polychaeta) from south America

*Paulo da Cunha LANA* and Claudia Silvia BREMEC***

* Centro de Estudos do Mar, Universidade Federal do Paraná
Av. Beira-Mar, s/n, 83255-000 Pontal do Sul, Paraná, Brazil
** Instituto Nacional de Investigacion y Desarrollo Pesquero
C. C. 175, 7600 Mar del Plata, Argentina

ABSTRACT

This paper summarizes the present taxonomic knowledge of Sabellariidae Johnston, 1865 from South America. Records of *Idanthyrsus armatus* Kinberg, 1867, *I. pennatus* (Peters, 1854), *Phragmatopoma attenuata* Hartman, 1944, *P. peruensis* Hartman, 1944, *P. virgini* Kinberg, 1867, *P. moerchi* Kinberg, 1867, *P. lapidosa* Kinberg, 1867, *Sabellaria bella* Grube, 1870, *S. bellis* Hansen, 1882, *S. fissidens* Grube, 1870, *S. minuta* Carrasco & Bustos, 1981, *S. nanella* Chamberlin, 1919, and *S. wilsoni* Lana & Gruet, 1989 are included. Regional synonymies, diagnoses, taxonomic remarks, and occurrence information are provided for each species, together with an identification key and distributional maps. Discontinuous distribution patterns of the continental sabellariid fauna may be only partially attributed to incomplete sampling. Many species seem to have restricted distribution ranges. It is hypothesized that the dispersion patterns of sabellariids in South America do not conform to the dispersal paradigm that could be expected from their active larval phases.

RÉSUMÉ

**Sabellariidae (Annelida, Polychaeta) d'Amérique du Sud**

L'état actuel des connaissances sur les Sabellariidae Johnston, 1865 d'Amérique du Sud est présenté. Les lieux de récoltes de *Idanthyrsus armatus* Kinberg, 1867, *I. pennatus* (Peters, 1854), *Phragmatopoma attenuata* Hartman, 1944, *P. peruensis* Hartman, 1944, *P. virgini* Kinberg, 1867, *P. moerchi* Kinberg, 1867, *P. lapidosa* Kinberg, 1867, *Sabellaria bella* Grube, 1870, *S. bellis* Hansen, 1882, *S. fissidens* Grube, 1870, *S. minuta* Carrasco & Bustos, 1981, *S. nanella* Chamberlin, 1919 et *S. wilsoni* Lana & Gruet, 1989 sont donnés. Les synonymies pour cette région, des diagnoses, des remarques taxonomiques et des informations sur les récoltes de chaque espèce sont fournies. Une clé d'identification des espèces et des cartes de distributions sont également données. La distribution discontinue observée le long des côtes d'Amérique du Sud pourrait être due à l'absence d'observations dans certaines régions. Cependant, beaucoup d'espèces semblent avoir une distribution réduite. L'hypothèse selon laquelle le mode de dispersion des Sabellariidae d'Amérique du Sud n'est pas conforme au modèle correspondant à une vie larvaire active est avancée.

## INTRODUCTION

The Sabellariidae Johnston, 1865 currently comprises seven genera and about 65 species of colonial or non-colonial tube-building worms. Some species construct reefs of great extent in temperate or tropical regions.

LANA P., & C. S. BREMEC, 1994. — Sabellariidae (Annelida: Polychaeta) from south America. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 211-222 Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

Representatives of this family occur from nearshore to oceanic depths (UEBELACKER, 1984).

The present recognized genera are *Phalacostremma* Marenzeller, 1895, *Monorchos* Treadwell, 1926, *Gunnarea* Johansson, 1927, *Lygdamis* Kinberg, 1867, *Idanthyrsus* Kinberg, 1867, *Phragmatopoma* Moerch, 1863, and *Sabellaria* Savigny, 1818, with only the three latter previously reported from South America. The regional sabellariid fauna was hitherto poorly known. Relevant taxonomic literature is widely scattered and the level of consistency in identifications appears to be rather low.

In this paper, we summarize the present taxonomic knowledge of Sabellariidae in South America. We have attempted to include all published records from this area. Synonymies, diagnoses and the known geographic range are provided for each species, together with an identification key and distributional maps.

This work is partially based on literature information, and we have not attempted to resolve disputed taxonomic problems. Some taxonomic assignments are tentative, but can serve as background information for future revisions based upon type-specimens or topotypes. Specific names are cited as listed in the original references.

## SYSTEMATICS

### *Idanthyrsus* Kinberg, 1867

Type-species: *Idanthyrsus armatus* Kinberg, 1867

### ***Idanthyrsus armatus*** Kinberg, 1867

*Idanthyrsus armatus* Kinberg, 1867: 349. — JOHANSSON, 1927: 90. — MONRO, 1930: 177, fig. 73. — MONRO, 1933: 1066, fig. 14. — MONRO, 1936: 172. — HARTMAN, 1944: 336, pl. 31, fig. 36. — HARTMAN, 1953: 10. — HARTMAN, 1966: 73, pl. 24, figs 2-6. — HARTMAN, 1967: 150. — RINGUELET, 1969: 212. — FAUCHALD, 1972: 530, pl. 55, figs h-j. — ORENSANZ, 1974: 55. — FAUCHALD, 1977: 54. — RULLIER & AMOUREUX, 1979: 188. — CARRASCO & BUSTOS, 1981: 170, figs 8-11. — HARTMANN-SCHRÖDER, 1983: 271. — LAVERDE-C, 1986: 128.

*Pallasia sexungula* — Ehlers, 1897: 125, pl. 8, figs 194-202. — EHLERS, 1900: 220. — EHLERS, 1901a: 267.

*Pallasia armata* — EHLERS, 1901b: 195.

*Sabellaria macropalea* — PRATT, 1901: 13, *pro parte*

*Pallasia pennata* — FAUVEL, 1941: 291.

**Diagnosis** — External paleae directed outward and plumelike, serrated, with a nearly straight shaft; spinelets widely separated and curved outward (Fig. 1a). Inner paleae smooth hooks with narrow transverse striae. Uncini with a double lateral row of 8 teeth, in addition to one median tooth at superior end. 2-4 pairs of nuchal hooks. Maximum reported length 59 mm.

**Distribution** — South America: Pacific coast of Colombia; Valparaiso, Concepcion, and other sites of Central Chile; Magellan Strait; Beagle Channel; Cape Horn; Malvinas-Falkland Islands; South Georgia Island; continental shelf off Patagonia and northern Argentina. Other records: Western Mexico; British Columbia; Alaska; Australia; Japan.

**Remarks** — *I. armatus* has been usually reported from cold waters in the southern and northern sectors of the Pacific and in the southern West Atlantic. The range of the closely related *I. pennatus* (Peters, 1854) appears to be circumtropical, extending northward or southward from that of *I. armatus*. The zones of overlapping are few and have been reported by MONRO (1933), RIOJA (1962), FAUCHALD (1977), and LAVERDE-CASTILLO (1986) for the Pacific coasts of Mexico, Panama and Colombia. However, records of *I. armatus* from Panama are doubtful, since Gorgona Island, cited in the literature as a Panamian locality (MONRO, 1933; FAUCHALD, 1977) is in fact off the Colombian coast, about 600 km south of the Canal Zone. In addition, MONRO's illustration of an external opercular palea (1933, p. 1065) clearly differs from those later provided by HARTMAN (1944) or DAY (1967).

Neither *I. armatus* nor *I. pennatus* have been recorded from the extensive tropical and subtropical Brazilian coast. The northern range of *I. armatus* along the Western Atlantic is clearly conditioned by the Subtropical Convergence, north of La Plata River, where the colder waters of the Malvinas-Falklands Current meet the more saline and warmer waters of the Brazil Current.

*I. armatus* and *I. pennatus* are known to differ only in minor details of the outer paleae dentation, tapering in the first and slender in the second. Besides that, shafts of the outer paleae are curved in *I. pennatus* and straighter in *I. armatus*. Temperature dependent variation in the morphology of polychaete hard parts has been previously

Source : MNHN, Paris

described by REISH (1977). A careful analysis of this problem should be undertaken in order to clarify the taxonomic relationships of those species.

***Idanthyrsus pennatus*** (Peters, 1854)

*Sabellaria (Pallasia) pennata* Peters, 1854: 613.
*Idanthyrsus regalis* — Chamberlin, 1919: 487, pl. 74, figs 1-8.
*Idanthyrsus pennatus* — JOHANSSON, 1927: 88. — MONRO, 1930: 176. — MONRO, 1933: 1065, fig. 13. — HARTMAN, 1939: 19. — FAUCHALD & REIMER, 1975: 90. — FAUCHALD, 1977: 54. — LAVERDE-CASTILLO, 1986: 128.

**Diagnosis** (modified from DAY, 1967) — Opercular crown with two rows of long paleae. External paleae with curved shafts and slender denticles (Fig. 1b). Inner paleae smooth with tapering tips. 1-2 pairs of stout nuchal hooks.

**Distribution** — South America: Pacific coast of Colombia and Ecuador; Galapagos Islands. Other records: Western Panama and Mexico; Mossambique; South Africa; Tropical Indo-West Pacific from Madagascar to Japan.

**Remarks** — Taxonomic affinities and distribution range of *I. pennatus* and *I. armatus* were discussed above.

*Phragmatopoma* Moerch, 1863

Type-species: *Phragmatopoma caudata* Moerch, 1863

***Phragmatopoma attenuata*** Hartman, 1944

*Phragmatopoma attenuata* Hartman, 1944: 352, pl. 38, figs 90-96, pl. 39, figs 100-101. — FAUCHALD, 1977: 54. — LAVERDE-CASTILLO, 1986: 128.
*Sabellaria (Phragmatopoma) virgini* — MONRO, 1933: 1062, fig. 11.

**Diagnosis** (modified from HARTMAN, 1944) — Opercular crown slender, prolonged and asymetrical in lateral view. External opercular paleae with a unique distal appendage, consisting of a palmately filamentous membrane, directed nearly at right angles to the main shaft. Shaft with a recurved tooth on the ventral-facing side and weakly scabrous on the upper surface (Fig. 1c).

**Distribution** — South America: Ecuador, Pacific coast of Colombia. Other records: Pacific side of Panama.

**Remarks** — As far as we know, there were no additional records of *P. attenuata* since Hartman's original description, based upon material collected by the Allan Hancock Pacific Expeditions along the Pacific coast of Colombia and Ecuador.

Material from Perlas Islands (Pacific side of Panama), originally referred to *Sabellaria (Phragmatopoma) virgini* by MONRO (1933), was correctly ascribed to *P. attenuata* by HARTMAN (1944). The original drawing of an external palea by MONRO (1933, p. 1063) was shown to be slightly misleading by FAUCHALD (1977), who re-examined the material from Perlas Islands and noticed the presence of two distinct teeth on either side of the distal plumes.

***Phragmatopoma peruensis*** Hartman, 1944

*Phragmatopoma peruensis* Hartman, 1944: 353, pl. 37, figs 84-85, pl. 39, fig. 99, pl. 41, fig. 104.

**Diagnosis** (modified from HARTMAN, 1944) — Very small size, less than 10 mm long. Shaft of external paleae with long, spatulate, distally rounded terminal membrane, strongly curved inward (Fig. 1d). Middle paleae with a conspicuous shoulder at their external edge.

**Distribution** — Peru.

**Remarks** — As *P. attenuata*, *P. peruensis* seems to be known only from through HARTMAN's original description.

***Phragmatopoma virgini*** Kinberg, 1867

*Phragmatopoma virgini* Kinberg, 1867: 349. — KINBERG, 1910: 70, pl. 27, fig. 4. — JOHANSSON, 1926: 2, fig. 1(1a-b). — JOHANSSON, 1927: 100. — HARTMAN, 1944: 351, pl. 35, figs 77-78. — HARTMANN-SCHRÖDER, 1962: 155, fig. 202 (as *Phragmatopoma* c.f. *virgini* — HARTMAN, 1966: 75, pl. 24, figs 6-8. — RINGUELET, 1969: 213.- ORENSANZ, 1974: 55, *pro parte*.

Source : MNHN, Paris

*Sabellaria macropalea* — PRATT, 1901: 13, *pro parte*.

**Diagnosis** — Opercular crown subcircular. External opercular palea with only two main teeth along outer margins, without any process between them (Fig. 1e). Middle paleae smooth, very fine and terminating in a hook. Abdominal uncini with 6 teeth. Maximum reported length 25 mm.

**Distribution** — Buket Island, San Nicolas Bay, Southern Chile (also spelt Bucket Island by earlier authors, this site is probably Sanchez Island, according to HARTMAN, 1966, p. 1); Ramuncho, near Concepcion, Central Chile; Malvinas-Falkland Islands.

**Remarks** — *P. virgini* was originally described from the Strait of Magellan, near Buket Island (= Sanchez Island), southern Chile. KINBERG (1867) referred to the number and aspect of external paleae ("externae 66 truncate, spina elongata armatae...") but provided no drawings. EHLERS (1901b) re-examined the type material and considered his species *Hermella orbifera* (Ehlers, 1901a) a synonym of *Sabellaria virgini* (Kinberg), since he did not recognize the name *Phragmatopoma*. However, in the redescription carried out with complementary specimens from southern Chile, EHLERS (1901b) figured external opercular paleae with sulcate median processes (pl. XXIII, fig. 11). The type specimen of *P. virgini* was posteriorly studied by JOHANSSON (1926) and HARTMAN (1944). Both described external paleae with only two main teeth along their outer, distal margins, without dentations or a flange between them. HARTMAN (1944) explicitly remarked that there was no indication of an attached flange or other structure along the concave edge. So, the presence of a median process in the external paleae can be considered a useful diagnostic character to distinguish *P. virgini* and *P. moerchi*. Consequently, the material that EHLERS (1901b) referred to *S. virgini* belongs in fact to *P. moerchi*, as already suggested by HARTMAN (1944). ORENSANZ (1974) mentioned *P. virgini* in a list of magellanic species, but according to the provided synonymy he also included earlier findings (EHLERS, 1901a; MONRO, 1936) which in fact correspond to *P. moerchi*.*P. virgini* is an intertidal species, known mainly from southern and central Chile. The Malvinas-Falkland Islands citation (PRATT, 1901; HARTMAN, 1944) represents its unique record from the Atlantic ocean.

### ***Phragmatopoma moerchi*** Kinberg, 1867

*Phragmatopoma moerchi* Kinberg, 1867: 349. — HARTMAN, 1944: 350,pl. 35, fig. 76, pl. 36, figs 80-83, pl. 39, figs 97-98. — HARTMANN-SCHRÖDER, 1960: 38. — HARTMANN-SCHRÖDER, 1962: 154, fig. 201. — HARTMANN-SCHRÖDER, 1965: 304.

*Phragmatopoma morchii* — JOHANSSON, 1926:4, fig. 1(2-8). — JOHANSSON, 1927: 101.

*Hermella orbifera* — Ehlers, 1901a: 267.

*Sabellaria virgini* — EHLERS, 1901b: 199, pl. 23, figs 1-4, 7-12, pl. 24, figs 1-5, *pro parte* (*non* KINBERG, 1867).

? *Sabellaria (Phragmatopoma) moerchi* — MONRO, 1936: 171.

*Phragmatopoma virgini* — ORENSANZ, 1974: 55, *pro parte*.

**Diagnosis** — Opercular crown flat and subcircular. External opercular paleae with a rectangular flange, frayed at the distal end (Fig. 1f). Middle paleae transversely rugose and slightly roughened on the outer side, terminating in a hook. Maximum reported length 50 mm.

**Distribution** — South America: Peru; northern and central coasts of Chile; Patagonia (?). Other records: Hawaii.

**Remarks** — *P. moerchi* is an intertidal and subtidal species, known from Peru to Chile and west to Hawaii. *Sabellaria (Phragmatopoma) moerchi* described by MONRO (1936) from 43°50' S - 65°01' 51" W (near Dos Bahias Cape, off Patagonia) could be referred to *P. moerchi*, since this author found " ... large comb-like processes ..." in the external opercular paleae. This would be the only record of the species in the Atlantic Ocean. However, MONRO (1936, p. 15) remarked that he could " ... find nothing significant to distinguish this species from JOHANSSON's account of KINBERG's *Phragmatopoma lapidosa*". We think that this material should be reviewed before the distribution range of *P. moerchi* is extended to the Atlantic.

### ***Phragmatopoma lapidosa*** Kinberg, 1867

*Phragmatopoma lapidosa* Kinberg, 1867: 349. — JOHANSSON, 1926: 2. — JOHANSSON, 1927: 99. — HARTMAN, 1944: 348, pl. 35, figs 73-75, pl. 36, fig. 79, pl. 40, figs 102-103. — AMARAL, 1987: 471, figs. 1-5.

? *Sabellaria fauveli* — Gravier, 1909: 650, pl. 18, figs 60-69.

Source : MNHN, Paris

**Diagnosis** — External paleae with a long conspicuous pinnate plume arising close to the upper distal margin of the palea (Fig. 1g). Middle paleae strong, uncinate, with a basal tooth. Inner paleae similar, but smaller. Uncini with 8 teeth. Maximum reported length 25 mm.

**Distribution** — South America: SE Brazil (from Rio Grande do Sul to Rio de Janeiro, and probably northward); Peru (?). Other sites: Caribbean; Atlantic coast of Mexico; Florida.

**Remarks** — A number of other forms, including *P. caudata* Moerch, 1863 (from the West Indies), *Sabellaria (Pallasia) castelnaui* Grube, 1870 (from New Zealand), *S. fauveli* Gravier, 1909 (from Peru) and *Centrocorone spinifera* Treadwell, 1939 (from Porto Rico), have been referred to *P. lapidosa* by JOHANSSON (1927) and HARTMAN (1944). In our opinion, this material, especially the records from the Pacific, needs reexamination. *P. lapidosa* is one of the most conspicuous polychaete species along the tropical and subtropical coasts of the Western Atlantic, building sandy reefs of great extent in the lower intertidal and shallow subtidal zones of exposed rocky beaches. If really present on the Pacific coast of South America, it should have been consistently reported by other authors. AMARAL (1987) provided a brief characterization of the species, based upon material collected along the southeastern coast of Brazil. However, her drawing of an external palea is slightly misleading, since the teeth of the prolonged plume are depicted as round and not tapering.

### *Sabellaria* Savigny, 1818

Type species: *Sabellaria alveolata* L., 1767

### ***Sabellaria bella*** Grube, 1870

*Sabellaria bella* Grube,1870: 69. — AUGENER,1934: 151, fig. 31a-d. — GRUET & LANA, 1988: 32, figs 1-2.
*Sabellaria alcocki* — RULLIER & AMOUREUX, 1979: 187, *pro parte* (*non* GRAVIER, 1906).

**Diagnosis** — External paleae asymetrical, with 2-3 lateral spines on each side of a central spike with 5-6 lateral teeth (Fig. 1h). Middle paleae alternate long (narrow, basally excavated, with a fine point) and short (spoon-shaped, crenulated). Inner paleae geniculate, basally excavated and distally serrated. Uncini with 6 (seldom 5) teeth.

**Distribution** — SE Brazil (Espirito Santo to Santa Catarina States).

**Remarks** — The opercular paleae were redescribed by GRUET & LANA (1988). Previous records from North Carolina and Peru (HARTMAN, 1944) were considered doubtful, on the basis of inner paleae morphology.

### ***Sabellaria bellis*** Hansen, 1882

*Sabellaria bellis* Hansen, 1882: 19, pl. 6, figs 5-17. — AUGENER, 1934: 149, fig. 30a-e. — HARTMAN, 1944: 339, pl. 30, figs. 27-29.— RULLIER & AMOUREUX, 1979: 188. — GRUET & LANA, 1988: 34, figs 3-4.

**Diagnosis** — External paleae with a broad spiny median spike and two lateral teeth, rarely a small additional one (Fig. 1i). Middle paleae all of the same length, short, spoon-shaped and laterally crenulated. Inner paleae long, concave and distally spiny.

**Distribution** — SE Brazil (Rio de Janeiro and Santa Catarina States).

**Remarks** — Opercular paleae were also redescribed and illustrated by GRUET & LANA (1988), who restricted the present distribution range of *S. bellis* to the southeastern Brazilian coast.

### ***Sabellaria fissidens*** Grube, 1870

*Sabellaria fissidens* Grube, 1870: 69. — EHLERS, 1901b: 196, pl. 24, figs 6-16. — RINGUELET, 1969: 213.

**Diagnosis** (modified from EHLERS, 1901b) — External paleae with distal serrations and a simple, bifurcated tip (Fig. 1j). Middle paleae concave, all of the same length. Inner paleae distally simple. Uncini with 7 teeth. Maximum reported length 28,5 mm.

**Distribution** — Coast of Chile, without reference to type- locality; Patagonic littoral (?).

**Remarks** — The presently available descriptions of *S. fissidens* correspond to the original material (GRUBE, 1870), fully redescribed by EHLERS (1901b). RINGUELET (1969) reported the species from the Patagonic littoral, but provided no descriptions or illustrations.

Source : MNHN, Paris

### *Sabellaria minuta* Carrasco & Bustos, 1981

*Sabellaria minuta* Carrasco & Bustos, 1981: 167, figs 1-7.

**Diagnosis** — External paleae serrate, with a long median spike with bifid serrations (Fig. 1k). Middle paleae alternating long and short. Inner paleae concave and distally simple. Uncini with 5-6 teeth. Probably the smallest species of the genus, with a maximum reported length of 7 mm.

**Distribution** — Continental shelf off Central Chile, near Concepcion, at 135 and 220 m depth.

**Remarks** — *Sabellaria minuta* is known only from the original description. This is the only record, besides *S. fissidens*, of the genus along the Pacific coast of South America.

### *Sabellaria nanella* Chamberlin, 1919

*Sabellaria nanella* Chamberlin, 1919: 261, pl. 2, figs 5-7. — HARTMAN, 1938: 16, pl. 3, figs 8-10. — HARTMAN, 1944: 340, pl. 30, figs 18-20. — HARTMAN, 1969: 509, figs 1-4. — RULLIER & AMOUREUX, 1979: 188. — LANA & GRUET, 1989: 243.

**Diagnosis** — External paleae directed outwards, with terminal smooth spikes terminating in a hook; a median spike stronger and situated in a different plane (Fig. 1l). Middle paleae concave and distally flat. Inner paleae concave, tapering to a point. Uncini with five teeth in two lateral rows and one tooth at superior extreme. Maximum reported length 18,5 mm.

**Distribution** — South America: SE Brazil (off Espirito Santo and Rio de Janeiro States); Argentina (Monte Hermoso, near Bahia Blanca). Other records: California.

**Remarks** — According to GRUET (pers. com.) and BREMEC (pers. obs.), material from South America appears to be morphologically indistinguishable from the type-material, originally described from California.

### *Sabellaria wilsoni* Lana & Gruet, 1989

*Sabellaria wilsoni* Lana & Gruet, 1989: 239, figs 1-21.

? *Sabellaria spinulosa* var. *alcocki* — FAUVEL, 1919: 477.

**Diagnosis** — Outer paleae assymetrical, distally flattened and spinous, with a central penicillate spike (Fig. 1m). Middle paleae of a single kind, directed upward, basally concave with two lateral expansions. Inner paleae pointing inwards, geniculated, basally excavated and distally pointed. Uncini with five teeth in two lateral rows, two or more teeth at posterior end, one median tooth at anterior end. Maximum reported length 22 mm.

**Remarks** — Dr. Mary PETERSEN (in litt.), from the Zoological Museum of Copenhagen, has called our attention to the close similarity between *S. wilsoni* and *S. vulgaris beaufortensis*. She kindly provided us with a set of unpublished drawings of *S. vulgaris* and *S. vulgaris beaufortensis* from North Carolina and Nova Scotia. *S. wilsoni* clearly differs from the North-American material in that its middle paleae are long and nearly straight, while those of *S. vulgaris* and *S. vulgaris beaufortensis* are much shorter and sharply recurved at the distal end.

Two specimens of *Sabellaria spinulosa alcocki* reported in FAUVEL (1919) from the French Guiana and mounted on a slide (n. C78, Laboratoire of Zoology, IRFA, Angers, France) were reexamined by LANA & GRUET (1989) and found to be identical to *S. wilsoni*. If confirmed through the observation of additional material, this record will greatly extend the northern range of *S. wilsoni*.

**Comments on other records of *Sabellaria* from South America** — Two specimens from the eastern Brazilian coast reported as *Sabellaria alcocki* by RULLIER & AMOUREUX (1979), were shown to belong in fact to *S. bella* and *S. wilsoni* (LANA & GRUET, 1989). As remarked above, *S. spinulosa alcocki*, reported from the French Guiana (FAUVEL, 1919), most probably belongs to *S. wilsoni*.

KEY TO SABELLARIIDAE FROM SOUTH AMERICA

| | | |
|---|---|---|
| **1a** | Opercular crown with two rows of paleae; a pair of large hooks *[Idanthyrsus]* | **2** |
| **1b** | Opercular crown with three rows of paleae; dorsal hooks absent | **3** |
| **2a** | External opercular paleae almost straight, with tapered lateral denticles or spinelets | *Idanthyrsus armatus* |
| **2b** | External opercular paleae with curved shafts and slender lateral denticles | *Idanthyrsus pennatus* |

Source : MNHN, Paris

**3a** Middle opercular paleae cover the inner ones; operculum a flattened cone *[Phragmatopoma]* ..... **4**
**3b** Middle opercular paleae not concealing the inner ones; operculum open *[Sabellaria]* ..... **8**

**4a** External opercular paleae without distal appendage ..... *Phragmatopoma virgini*
**4b** External opercular paleae with distal appendage ..... **5**

**5a** Distal appendage long, spatulate, distally rounded, with a smooth margin.... *Phragmatopoma peruensis*
**5b** Distal appendage pinnate or comb-like..... **6**

**6a** Distal appendage short, rectangular, with a frayed distal border ..... *Phragmatopoma moerchi*
**6b** Distal appendage long, pinnate or brush-like..... **7**

**7a** Distal appendage a long and nearly straight pinnate plume arising from the upper distal edge of the palea ..... *Phragmatopoma lapidosa*
**7b** Distal appendage a palmately filamentous membrane, brush-like, nearly at right angles to the main shaft ..... *Phragmatopoma attenuata*

**8a** Inner paleae distally serrated or frayed ..... **9**
**8b** Inner paleae distally simple or tapering to a point ..... **10**

**9a** Inner paleae distally serrated; middle paleae alternately long and short; external paleae assymetrical, with 2-3 lateral spines on each side of a central serrated spike, provided with 5-6 lateral teeth ..... *Sabellaria bella*
**9b** Inner paleae with about 6 distal spines; middle paleae all of the same length; external paleae with a broad spiny central spike and two (rarely a small additional one) teeth..... *Sabellaria bellis*

**10a** External paleae with distal processes in the same plane ..... **11**
**10b** External paleae with a strong median simple spike in a different plane ..... *Sabellaria nanella*

**11a** Median spike of outer paleae a simple, bifurcated tip ..... *Sabellaria fissidens*
**11b** Median spike of outer paleae with a conspicuous spiny process ..... **12**

**12a** Median spike with bifid serrations ..... *Sabellaria minuta*
**12b** Median spike penicillate ..... *Sabellaria wilsoni*

## BIOGEOGRAPHICAL COMMENTS

Thirteen species of Sabellariidae are presently known from South America (Fig. 2), five in the Atlantic, six in the Pacific with two in both oceans, not including some doubtful records mentioned above. *Idanthyrsus armatus* and *Phragmatopoma virgini*, the only species common to the two oceans, have been recorded mainly from the connected sectors of the South Atlantic and South Pacific, or near this area.

The existence of distinct sabellariid faunas along the two margins of the South American continent, with some degree of convergence towards its southern sector, can be attributed to prevalent oceanographic conditions. Subantarctic water is of lesser significance in the Atlantic, since South America, owing to its southeastward extent, deflects large quantities of colder waters along its west coast (SVERDRUP *et al.*, 1942). A tropical or subtropical sector along the Pacific is not as extensive as in the Atlantic, because of the Humboldt Current. Consequently, average water temperatures along the west coast of South America are lower than on the east margin.

HARTMANN-SCHRöDER (1960) recognized distinct north-temperate, tropical and south-temperate polychaete faunas in a zoogeographic analysis from Alaska to "Tierra del Fuego". With the current information, it is not yet possible to draw such putative boundaries for the regional sabellariid fauna. However, a group made up of *Phragmatopoma lapidosa* and a more diversified *Sabellaria* stock, dominant along the warmer waters of the Atlantic side north of 35° S, is clearly separated from an East Pacific and southern Atlantic group, represented by several *Phragmatopoma* species, besides *Idanthyrsus armatus*, *Sabellaria minuta* and *S. fissidens*.

Only *P. lapidosa*, *I. armatus* and *P. moerchi* have been consistently reported from extensive areas in the region. GRUET & LANA (1991) have suggested, in relation to *Sabellaria*, that the low number of described species and discontinuous distribution patterns, mainly along the Pacific coast, are probably due to incomplete sampling or

Source : MNHN, Paris

to a lack of suitable habitats. However, it is well known that many species of *Sabellaria* and *Phragmatopoma* are very conspicuous members of the rocky intertidal fauna, building sand-reefs of great extent. It would have been difficult to overlook them during the several faunal surveys carried out along both coasts of South America this century. We suggest that disjunct distribution, as currently reported for most species, is in fact an actual zoogeographical pattern of the continental sabellariid fauna.

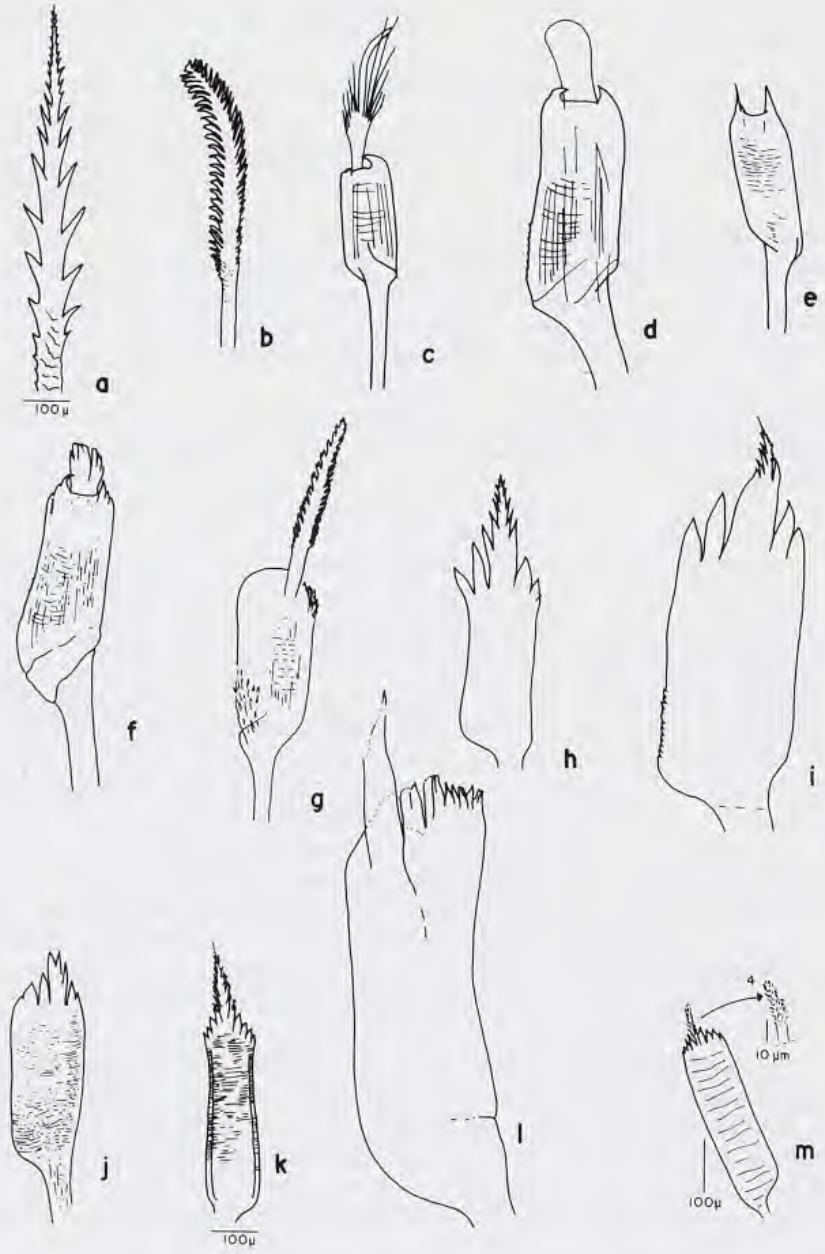



FIG. 1. — Outer opercular paleae of sabellariid species from South America. a: *Idanthyrsus armatus*. b: *I. pennatus*. c: *Phragmatopoma attenuata*. d: *P. peruensis*. e: *P. virgini*. f: *P. moerchi*. g: *P. lapidosa*. h: *Sabellaria bella*. i: *S. bellis*. j. *S. fissidens*. k: *S. minuta*. l: *S. nanella*. m: *S. wilsoni*.

Source : MNHN, Paris

Larval transport by wave currents has been considered the main recruitment source for benthic shelf species (JOSEFSON, 1985). One could expect that littoral surface currents be responsible for the continuous distribution of invertebrate fauna along continental shelves. This would be specially true concerning the dispersal of polychaete species with active larval phases, such as the sabellariids. Larval development, from fertilization to settlement, can take up to 32 weeks in warm-temperate sabellariid species, and 3-4 weeks in tropical species (ECKELBARGER, 1977). Yet, as shown above, continuous occurrence patterns are not a common feature among the local sabellariid fauna. A number of factors could account for this, both in large and small spatial scales. The circulation of the Pacific water masses is more sluggish than in the Atlantic and does not allow for an intense mixing of different water masses (SVERDRUP *et al.*, 1942). In addition, surface winds or inshore upwelling, present on both sides of the continent, have been previously shown to sweep away pelagic larvae of littoral forms (ROUGHGARDEN *et al.*, 1988). Large-scale physical-oceanographic processes which transport larvae farther offshore also appear to regulate latitudinal differences in the recruitment of marine invertebrates, mainly in the tropics (SUTHERLAND, 1990). Experimental evidence concerning sabellariid recruitment in small spatial scales has suggested that larvae respond first to proper flow conditions and only then to chemical cues that induce metamorphosis (PAWLIK *et al.*, 1991). Unlike the larvae of solitary sabellariid species, which show no preference for conspecific substrata, settlement of gregarious species seems to be highly dependent on the presence of conspecific reefs (PAWLIK, 1988). In this context, it is reasonable to suppose that the dispersion of colonial sabellariids is rather through reef accretion than through the formation of new reefs.

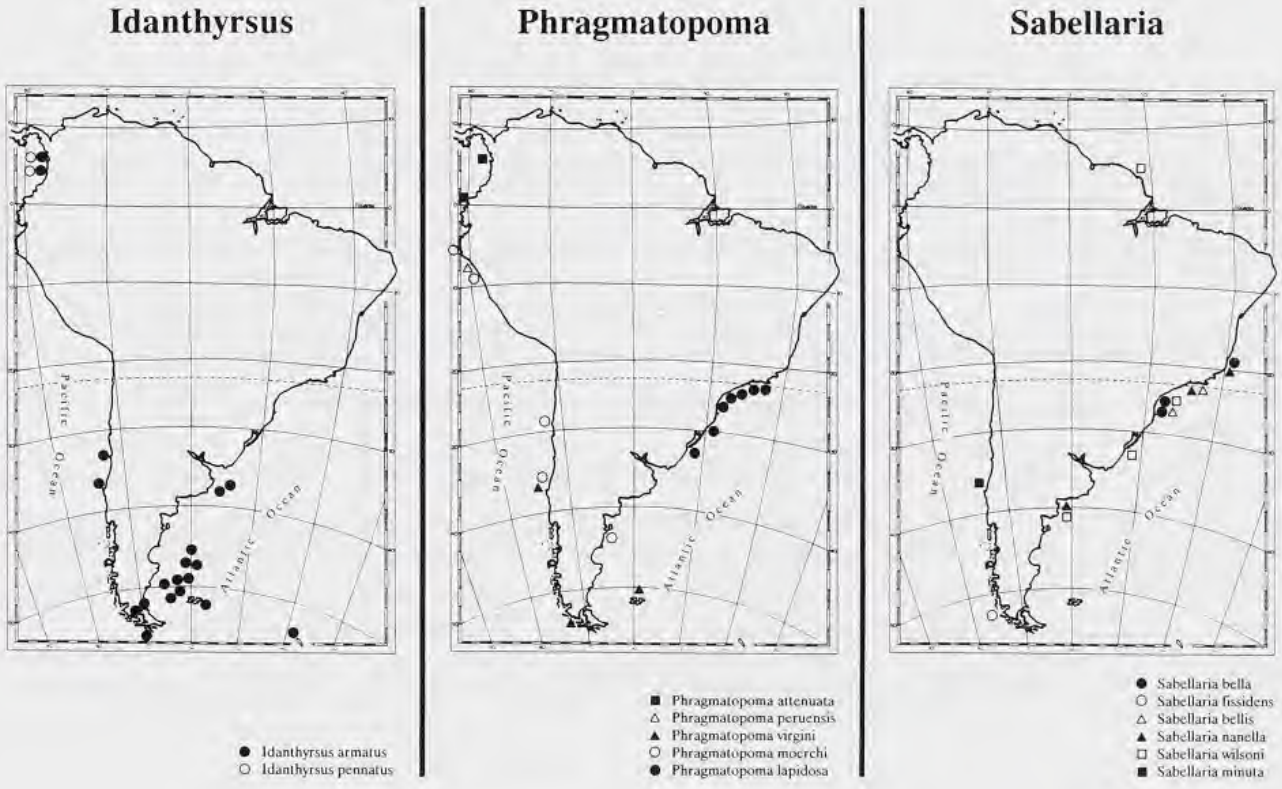



FIG 2. — Distribution of sabellariid species in South America.

Source : MNHN, Paris

All these factors may provide an explanation for the disjunt distribution patterns of the regional sabellariid fauna, through the restriction of stenothermic species dispersal. Despite the presence of extensive sandy reefs , distribution of sabellariids can in fact be determined by pre-settlement processes, such as local patterns of larval transport, which will affect larval survival and recruitment.

These results provide additional evidence in support of an alternate hypothesis to the dispersal paradigm for sabellariids, previously stated by FAUCHALD (1984). We suggest that sabellariids, contrary to what could be expected from their active dispersal phase, can in fact have endemic or geographically restricted distribution patterns.

## ACKNOWLEDGEMENTS

Our thanks to Lic. N. SCARLATTO, who translated German papers. Dr. Yves GRUET and Dr. Mary PETERSEN were most helpful in providing information concerning species of *Sabellaria*. The second author was partially supported by a grant from the Brazilian Research Council (CNPq).

## REFERENCES

AMARAL, A. C. Z., 1987. — Breve caracterização de *Phragmatopoma lapidosa* Kinberg, 1867 (Polychaeta, Sabellariidae). *Revta Bras. Zool., São Paulo*, **3** : 471-474.

AUGENER, H., 1934. — Polychaeten aus den Zoologischen Museen von Leiden und Amsterdam. 4. *Zool. Meded., Leiden*, **17** : 67-160.

CARRASCO, F. D. & BUSTOS, H. E. R., 1981. — Dos especies de poliquetos de la familia Sabellariidae, *Sabellaria minuta* sp. n. e *Idanthyrsus armatus* Kinberg epizoos de Crustaceos Decapodos. *Bol. Soc. Biol. Concepcion*, **51** : 167-173.

CHAMBERLIN, R. V., 1919. — Pacific coast Polychaeta collected by Alexander Agassiz. *Bull. Mus. Comp. Zool., Harvard*, **63** : 251- 276.

DAY, J. H., 1967. — *A monograph on the Polychaeta of Southern Africa*. British Museum Nat. Hist. Publ. 38, 878 pp.

ECKELBARGER, K. J., 1977. — Larval development of *Sabellaria floridensis* from Florida and *Phragmatopoma californica* from Southern California (Polychaeta: Sabellariidae), with a key to the sabellariid larvae of Florida and a review of development in the family. *Bull. Mar. Sc.*, **27** : 241-255.

EHLERS, E., 1897. — *Polychaeten. Hamburger Magalhaenischen Sammelreise*. Hamburg, Friedrichsen & Co., 148 pp.

EHLERS, E., 1900. — Magellanische Anneliden gesammelt wahrend der schwedischen Expedition nach den Magellanslandern. *Nachr. Kl. Ges. wiss., Gottingen*, 1900 : 206-223.

EHLERS, E., 1901a. — Die Anneliden der Sammlung Plate. *Fauna Chil., Zool. Jahrb.*, **5** : 251-272.

EHLERS, E., 1901b. — Die Polychaeten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch. *In*: *Festschrift zur Feier des Hundertfunfzigjahrigen Bestehens der koniglichen Gesellschaft der Wissenschaften zu Gottingen (Abh. Math.-Phys.)*. Berlin, Wiedmannsche Buchhandlung, 232 pp.

Source : MNHN, Paris

FAUCHALD, K., 1972. — Benthic polychaetous annelids from deep water off Western Mexico and adjacent areas in the Eastern Pacific Ocean. *Allan Hancock Monogr. mar. Biol.*, **7** : 1-575.

FAUCHALD, K., 1977. — Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. *Smithson. Contr. Zool.*, **221** : 1-81.

FAUCHALD, K., 1984. — Polychaete distribution patterns, or: can animals with Palaeozoic cousins show large-scale geographical patterns? In: P.A. HUTCHINGS (ed.), *Proc. First Intern. Polychaete Conf.*, Sydney, The Linnean Society of New South Wales : 1-6.

FAUCHALD, K. & REIMER, A. A., 1975. — Clave de poliquetos panamenos con la inclusion de una clave para todas las familias del mundo. *Bol. Inst. Oceanogr. Univ. Oriente*, **14** : 71-94.

FAUVEL, P., 1919. — Annélides Polychètes de la Guyane Francaise. *Bull. Mus. nat. Hist. nat. Paris*, **25** : 472-479.

FAUVEL, P., 1941. — Annélides Polychètes de la Mission du Cape Horn (1882-1883). *Bull. Mus. nat. Hist. nat. Paris*, **2** : 272-298.

GRAVIER, C., 1906. — Un Sabéllarien vivant sur un Brachiopode (*Kingena alcocki* Joubin). *Bull. Mus. Hist. nat. Paris*, **12** : 540- 543.

GRAVIER, C., 1909. — Annélides polychètes recueillies à Payta (Pérou) par le Dr. Rivet. *Arch. Zool. gen.exp., Paris*, **4** : 617-659.

GRUBE, A. E., 1870. — Uber die Goldkronchen (Sabellarien oder Hermellen). *Schles. Gesellsch. f. vaterl. Cultur.*, Jahres-Bericht **47** : 69-70

GRUET, Y. & LANA, P. C., 1988. — Remarks on the opercular paleae of *Sabellaria bella* Grube, 1870 and *Sabellaria bellis* Hansen, 1882 (Sabellariidae; Polychaeta) fom the southeast coast of Brazil. *Neritica, Pontal do Sul, PR*, **3** : 31-36.

GRUET, Y. & LANA, P.C., 1991. — Distribution of patterns of *Sabellaria* (Polychaeta; Sabellariidae) in South America. *Bull. Mar. Science*, **48** : 588.

HANSEN, A., 1882. — Recherches sur le Annélides recueillies par M. le Professeur Edouard Van Beneden pendant son voyage au Brésil et à la Plata. *Mem. Cour. Acad. Roy. Sci. Belgique, Bruxelles, Mém.*, **44** : 1-29, pls 1-7.

HARTMAN, O., 1938. — Annotated list of the types of polychaetous annelids in the Museum of Comparative Zoology. *Bull. Mus. Comp. Zool.*, Harvard, **85** :1-31.

HARTMAN, O., 1939. — The polychaetous annelids collected on the presidential cruise of 1938. *Smithson. Misc. Coll.*, **98** : 1-22.

HARTMAN, O., 1944. — Polychaetous Annelids, Part VI. Paraonidae, Magelonidae, Longosomidae, Ctenodrilidae and Sabellariidae. *Allan Hancock Pacific Exped.*, **10** : 311-389.

HARTMAN, O., 1953. — Non-pelagic polychaetes of the Swedish Antarctic Expedition. 1901-1903. *Furth. Zool. Swed. Antarct. Exped. 1901-1903*, **4** : 1-83.

HARTMAN, O., 1966. — Polychaeta Myzostomidae and Sedentaria of Antarctica. *Antarc. Res. Ser.*, **7** : 1-158.

HARTMAN, O., 1967. — Polychaetous Annelids collected by the USNS Eltanin and Staten Island cruises, chiefly fron Antarctic seas. *Allan Hancock Monogr. mar. Biol.*, **2** : 1-387.

HARTMAN, O., 1969. — Atlas of sedentariate polychaetous annelids from California. *Allan Hancock Foundation, Univ. Southern California, Los Angeles*, 812 pp.

HARTMANN-SCHROEDER, G., 1960. — Poliquetos de la costa occidental de América desde Alaska hasta Tierra del Fuego. *Actas y Trabajos del Primer Congreso Sudamericano de Zoologia*, **2** : 177-187.

HARTMANN-SCHRÖDER, G., 1962. — Die Polychaeten des Eulitorals. Zur Kenntnis des Eulitorals der chilenischen Pazifikkuste und der argentinischen Kuste Sudpatagoniens unter besonderer Berucksichtigung der Polychaeten und Ostracoden. *Mitt. Hamburg Zool. Mus. Inst.*, **60** : 57-167.

HARTMANN-SCHROEDER, G., 1965. — Die Polychaeten des Sublitorals. Zur Kenntnis des Sublitorals der chilenischen Kuste unter besonderer Berucksichtigung der Polychaeten und Ostracoden. *Mitt. Hamburg Zool. Mus. Inst.*, **62** (Suppl.) : 59-305.

HARTMANN-SCHROEDER, G., 1983. — Die Polychaeten der 15., 36. und 76. Reise von FFS "Walther Herwig" zum patagonischen Schelf (Sudwest-Atlantik). *Senckenbergiana marit.*, **15** : 251-277.

Source : MNHN, Paris

JOHANSSON, K., 1926. — Bemerkungen uber die Kinberg'schen Arten der Familien Hermellidae und Sabellidae. *Ark. Zool., Stockholm*, **18A** : 1-28.

JOHANSSON, K., 1927. — Beitrage zur Kenntnis der Polychaeten - Familien Hermellidae, Sabellidae und Serpulidae. *Zool. Bidrag, Uppsala*, **11** : 1-184.

JOHNSTON, G., 1865. — *A catalogue of the British non-parasitical worms in the collection of the British Museum*. London, 366 pp.

JOSEFSON, A. B., 1985. — Distribution of diversity and functional groups of marine benthic infauna in the Skagerrack (eastern North Sea). Can larval availability affect diversity? *Sarsia*, **70** : 229-249.

KINBERG, J. G. H., 1867. — Annulata Nova. *Ofv. Kongl. Vetensk. Akad. Forth., Stockholm*, **23** : 337-357.

KINBERG, J. G. H., 1910. — Annulater. Kongliga Svenska Fregatten "Eugenies" Resa omkring jorden under befal af C.A.Virgin aren 1851-1853. *Vetenskapliga Iakttagelser pa Konung Oscar den Forstes Befallning Utgifna af K. Svenska Vetenskapsakademien Zoology*, **3** :33-78.

LANA, P. C. & GRUET, Y., 1989. — *Sabellaria wilsoni* sp.n. (Polychaeta, Sabellariidae) from the southeast coast of Brazil. *Zool. Scr.*, **18** : 239-244.

LAVERDE-CASTILLO, J. J. A., 1986. — Lista anotada de los poliquetos (Annelida) registrados para el Pacifico colombiano, con notas preliminares sobre su zoogeografia. *Actual. Biol., Bogota*, **15** : 123-130.

MARENZELLER, E.von., 1895. — *Phalacrostemma cidariophilum*, eine neue Gattung und Art der Hermelliden. *Akad. Wiss. Wien, Anz.*, **32** : 191-192.

MOERCH, O. A. L., 1863. — Revisio critica Serpulidarum. Et Bidrag til Rorormenes Naturhistorie. *Naturhist. Tidssk. Stiftet at H. Kroyer, Copenhagen*, **3** : 347-470.

MONRO, C. C. A., 1930. — Polychaete worms. *Discovery Rep.*, **2** : 1-222.

MONRO, C. C. A., 1933. — The Polychaeta Sedentaria collected by Dr. C. Crossland at Colon, in the Panama Region, and The Galapagos Islands during the Expedition of the S.Y.'St.George'. *Proc. Zool. Soc. London*, 1933 : 1039-1092.

MONRO, C. C. A., 1936. — Polychaete worms II. *Discovery Reports* **12** : 59-198.

ORENSANZ, J. M., 1974. — Los anelidos poliquetos de la Provincia Biogeografica Magallanica. I. Catalogo de las especies citadas hasta 1974. *Lab. Comunid. Benton. Contrib. Tecnica*, **1** : 1-83 pp.

PAWLIK, J. R., 1988. — Larval settlement and metamorphosis of Sabellariid Polychaetes with special reference to *Phragmatopoma lapidosa*, a reef-building species, and *Sabellaria floridensis*, a non gregarious species. *Bull. mar. Science*, **43** : 41-60.

PAWLIK, J. R., BUTMAN, C. A. & STARCZAK, V. R., 1991. — Hydrodynamic facilitation of gregarious settlement of a reef-building tube worm. *Science*, **251** : 327-331.

PETERS, W. C. H., 1854. — Naturwissenschaftliche Reise nach Mosambique in 1842 bis 1848 ausgefuhrt. *Akad. Wiss. Berlin. Monatsber.*, 1854 : 610-614.

PRATT, E., 1901. — A collection of Polychaeta from the Falkland Islands. *Manchester Lit. and Philos. Soc. Mem. Proc.*, **45** : 1- 18.

REISH, D. J., 1977. — The role of life story studies in polychaete systematics. *In*:D.J. REISH & K. FAUCHALD (eds), *Essays on polychaetous annelids in memory of Dr. Olga Hartman. Allan Hancock Fdn*, University of Southern California, pp. 461-476.

RINGUELET, R. A., 1969. — Clave o llave para el reconocimiento de familias y generos de poliquetos del litoral atlantico argentino. *Acta Zool. Lilloana*, **24** : 193-218.

RIOJA, E., 1962. — Estudios anelidologicos. XXVI. Algunos anelidos poliquetos de las costas del Pacifico de Mexico. *An. Inst. Biol. Univ. Mexico*, 33 : 131-229.

ROUGHGARDEN, J., GAINES, S. D. & POSSINGHAM, H., 1988. — Recruitment dynamics in complex life cycles. *Science*, **241** : 1460- 1466.

RULLIER, F. & AMOUREUX, L., 1979. — Campagne de la Calypso au large des côtes atlantiques de l'Amérique du sud (1961-1962). I.33. Annélides Polychètes. *Ann. Inst. océanogr., Monaco*, **55** (Suppl.) : 145-206.

Source : MNHN, Paris

SAVIGNY, J. S., 1818. — Les annélides. *In*: *Histoire naturelle des animaux sans vertèbres*. J. B. Lamarck. Paris, J. B. Baillière Librairie, **5** : 274-374.

SUTHERLAND, J.P., 1990. — Consequences of recruitment variation on rocky shores of the eastern Pacific Ocean. *Publicação ACIESP, Sao Paulo*, **71** : 43-66.

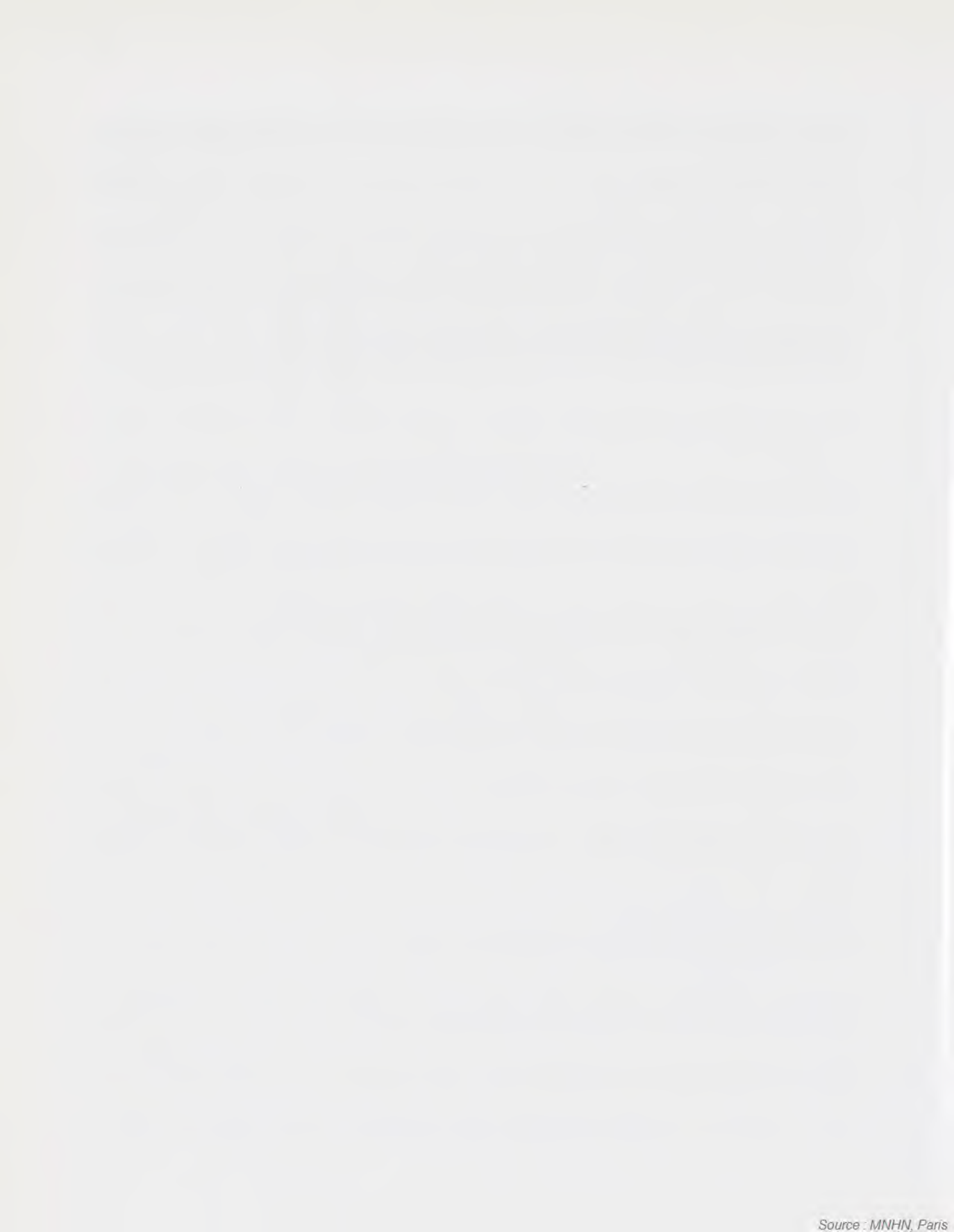
SVERDRUP, H. U., JOHNSON, M. W. & FLEMING, R. H., 1942. — *The Oceans*. Prentice-Hall, Inc. New Jersey, 1087 pp.

TREADWELL, A.L., 1926. — Contributions to the zoology of the Philippine Archipelago and adjacent regions. Additions to the polychaetous annelids collected by the U.S. fishery steamer *Albatross*. *U. S. Nat. Mus., Bull.*, vol. **100** : 183-193.

TREADWELL, A.L., 1939. — New polychaetous annelids from New England, Texas and Puerto Rico. *Amer. Mus. Novitat., New York*, 1023 : 1-7.

UEBELACKER, J. M., 1984. — Family Sabellaridae. *In*: J. M. UEBELACKER & P.G. JOHNSON (eds), *Taxonomic guide to the polychaetes of the northern Gulf of Mexico*. Barry A. VITTOR & Associates, Mobile, **49** : 1-10.

Source : MNHN, Paris



Source : MNHN, Paris

# The phylogenetic position of the Pilargidae with a cladistic analysis of the taxon – facts and ideas

*Frank LICHER & Wilfried WESTHEIDE*

Universität Osnabrück, Fachbereich Biologie/Chemie, Spezielle Zoologie
D-49069 Osnabrück, Germany

ABSTRACT

The taxon Pilargidae is considered to be a group of derived hesionid species. This view is supported by the fact that apparent pilargid-specific features also occur in a few hesionid taxa. The idea is also based on the hypothesis that the pilargid stem species evolved by early maturation ("progenetically") of a juvenile stage of a large-bodied hesionid species. Making use of all characters available and using a hesionid taxon as outgroup, a cladogram of all pilargid genera was constructed with the program HENNIG 86, vers. 1.5. It shows well developed prostomial appendages and separate biarticulated palps to be the plesiomorphic character states. The genera *Synelmis* and *Litocorsa* are newly defined. For phylogenetic systematic implications the pilargid taxa should be included in the Hesionidae.

RÉSUMÉ

**Position phylogénétique des Pilargidae avec analyse cladistique du taxon - faits et idées.**

Le taxon des Pilargidae est considéré comme étant dérivé d'un groupe d'Hesionidae. Ce point de vue est conforté par le fait que des caractères typiques des Pilargidae se rencontrent également chez quelques Hesionidae. L'idée est basée sur l'hypothèse que l'espèce souche des Pilargidae a évolué à partir du stade juvénile d'un hésionide de grande taille qui aurait acquis une maturité sexuelle précoce (progenèse). En se fondant sur tous les caractères disponibles et en prenant un hésionide comme groupe extérieur, un cladogramme de tous les genres de Pilargidae a été construit à l'aide du programme HENNIG 86, version 1.5. Celà révèle que des appendices prostomiaux bien développés et les palpes biarticulés représentent l'état plésiomorphe. Les genres *Synelmis* et *Litocorsa* sont redéfinis. Dans une optique de systématique phylogénétique, les Pilargidae devraient être inclus dans les Hesionidae.

## INTRODUCTION

When he described *Pilargis verrucosa*, SAINT-JOSEPH (1899) erected the Pilargidae to contain it, starting a long-lasting discussion on the systematic validity of this polychaete taxon. The first descriptions of pilargid species were actually much earlier, but the authors considered the worms to be orbiniids (*Sigambra grubii* Müller,

LICHER, F. & W. WESTHEIDE, 1994. — The phylogenetic position of the Pilargidae with a cladistic analysis of the taxon – Facts and ideas. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 223-235. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

1858, as Amytidea; and *Parandalia tricuspis* Müller, 1858, as Ariciaea) or syllids (*Ancistrosyllis groenlandica* McIntosh, 1879; *Cabira incerta* Webster, 1879; *Pilargis tardigrada* (Webster, 1879), as *Phronia*; *Synelmis albini* (Langerhans, 1881), as *Ancistrosyllis*. EHLERS (1908) was the first to consider these species to be hesionids. For most polychaete taxonomists, however, these species appeared to be too different from "typical" hesionids to be included in this family. For instance, HESSLE (1925) argued that *Ancistrosyllis* was neither a syllid nor a hesionid - an opinion which has persisted to the present.

One of us (W.WESTHEIDE) became extremely interested in pilargids when first seeing living *Sigambra* individuals at the northern coast of China in 1987. The form of these specimens, under a low power dissecting microscope, and their locomotion seemed so similar to those features of the interstitial hesionid species *Hesionides maxima* Westheide, 1967 and *Hesionides pettiboneae* Westheide, 1987 (WESTHEIDE, 1967, 1987a) that the later identification of the fixed specimens as a pilargid taxon was rather astonishing. We asked ourselves whether our many years of experience in recognizing live meiofauna-taxa just by their appearance and locomotory characters had failed in this case or whether this apparent mistake might be due to a very close systematic relationship between interstitial hesionids and pilargids.

This prompted an investigation of the phylogenetic systematics within the Pilargidae to see if there was any support for this hypothesized relationship. Our findings resulted in reinvestigations of several pilargid taxa and a review of the entire pilargid literature, especially JONES (1961), EMERSON & FAUCHALD (1971), BRITAEV & SAPHRONOVA (1981), FITZHUGH & WOLF (1990) and SALAZAR-VALLEJO & SOLÍS-WEISS (1992). A comprehensive analysis of the taxon suffers from the fact that no true anatomical or any ultrastructural details are available. FITZHUGH & WOLF (1990) in their cladogram especially used brain gross morphology as a taxonomic and systematic character. Although it is based only on the outlines of various brains taken from whole mounted specimens their cladistic analysis has been of considerable help. However, we do not agree with their phylogenetic interpretation in all points. Our phylogenetic analysis differs from their results because we make use of a different outgroup.

## CLADISTIC ANALYSIS

DIAGNOSTIC FEATURES OF THE PILARGIDAE. — The pilargid body is cylindrical or dorsoventrally flattened, and anterior segments can be inflated. The integument may be smooth or papillated. The prostomium bears antennae (three, two, or none at all) and biarticulated palps, consisting of large palpophores and palpostyles of different length and shape. Small pigmented eyes may be present. The pharynx is eversible and usually has a circlet of distal papillae; jaws may be present.

The achaetous peristomium is usually equipped with two pairs of tentacular cirri, which may be absent. The parapodia are usually well developed and biramous. In most of the species the notopodia possess a single stout spine or hook, and a notoacicula; additional capillary chaetae may occur. The neuropodia are equipped with an acicula and several simple chaetae, which may be capillary, slightly unidentate, serrated, smooth, spinous or furcate. Dorsal and ventral cirri are usually present, and they may be of different lengths. Gills exist in one genus. The pygidium has two or three anal cirri.

The following characters are considered to be autapomorphic, defining the monophyly of the Pilargidae: (1) possession of a simple specific stout emergent notochaeta, to be reduced in some genera, (2) possession of exclusively simple, neuropodial mainly capillary chaetae, and (3) possession of fleshy biarticulated palps.

LIST OF PILARGID GENERA. — The assumed autapomorphies of the pilargid taxa are briefly mentioned; the material examined during this study is listed in brackets.

*Sigambra* Müller, 1858: this first described genus and most species-rich taxon of the family was recognized as a pilargid not earlier than in the middle of this century (HARTMAN, 1959; PETTIBONE, 1966). Since the notopodial hooks are considered by the authors to be plesiomorphic within the Pilargidae the taxon possesses primitive features only, but see FITZHUGH & WOLF (1990) (*Sigambra bassi* USNM 86966; *S. grubii* USNM 103016; *S. tentaculata*, USNM 86975; *S. wassi*, USNM 30987; specimens from Thailand and China).

*Ancistrosyllis* McIntosh, 1879: the monophyly of the taxon may be based on its five-lobed brain (FITZHUGH & WOLF, 1990). *Ancistargis* Jones, 1961, is tentatively included (PETTIBONE, 1966; GARDINER, 1976; WOLF, 1984), although the species of this genus are clearly separated from *Ancistrosyllis* in possessing two antennae only. If *Ancistargis* were accepted as a separate taxon, no synapomorphic character for *Ancistrosyllis*-species with three antennae would be available (*Ancistrosyllis breviceps* LACMNH AHF POLY 0143, LACMNH Velero st. 7498-

Source : MNHN, Paris

61; *A. carolinensis* USNM 86909; *A. hartmanae* USNM 30989; *A. papillosa* USNM 86923, and specimens from other sources).

*Cabira* Webster, 1879: the monophyly of this taxon is clearly shown by the possession of jaws (BRITAEV & SAPHRONOVA, 1981) (*Cabira incerta* USNM 30985).

*Pilargis* Saint-Joseph, 1899: since the papillated integument is considered to be a synapomorphy, this taxon should be closely related to *Ancistrosyllis-Ancistargis*, *Cabira* and *Paracabira*. A notopodial spine or hook is absent. As notopodia in all pilargid taxa - except *Otopsis* - are equipped with spines or hooks the absence of a chaetae of this kind in *Pilargis* is considered to be a derived character (*Pilargis berkeleyae* USNM 86959).

*Otopsis* Ditlevsen, 1917: the genus resembles *Synelmis*, but lacks notopodial spines or hooks, which is interpreted as a loss (see also *Pilargis*).

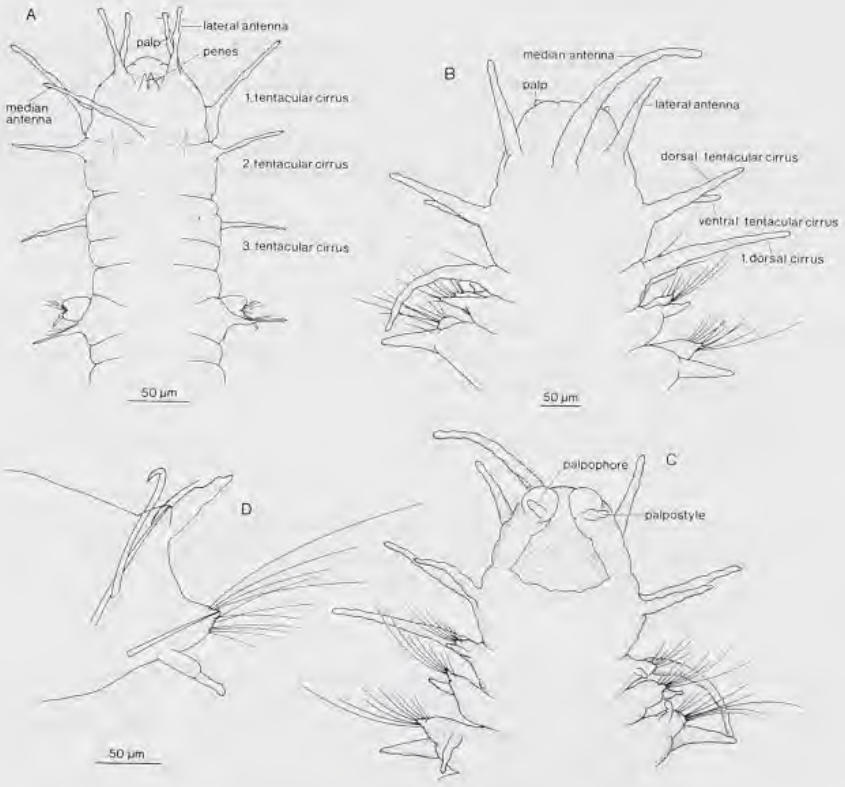



FIG. 1. — *Hesionides gohari* Hartmann-Schröder, 1960 and *Sigambra sp.* from Yellow Sea, near Qingdao: **a**, *Hesionides gohari*, anterior end, dorsal view. — **b**, *Sigambra sp.*, anterior end, dorsal view. — **c**, anterior end, ventral view. — **d**, parapodium, mid-body region.

*Synelmis* Chamberlin, 1919: we adopt the view of FITZHUGH & WOLF (1990) and partition *Synelmis* species between "complex A" (species with furcate neuropodial spines) and "complex B" (species with non-furcate neuropodial spines). The non-furcate, less complex chaetal type is considered to be the apomorphic character state. For the monophyly of the two *Synelmis* complexes see "Discussion" (*Synelmis albini*, collection of the senior author; *S. simplex*, USNM 19480).

*Talehsapia* Fauvel, 1932: this monotypic, poorly known taxon is included in the analysis although its assignment to the Pilargidae has been repeatedly questioned (e.g., PETTIBONE, 1966, EMERSON & FAUCHALD, 1971), mainly because of the possession of jaw-like structures. The shape of the body, especially of the anterior region, the absence of prostomial and tentacular appendages, the presence of an emergent notopodial spine, the absence of notoaciculae and dorsal cirri, and the possession of only simple chaetae suggest a close relationship

Source : MNHN, Paris

with the *Loandalia-Parandalia* complex. The possession of jaws is the autapomorphic character of this taxon; they differ distinctly from those in *Cabira*.

*Loandalia* Monro, 1936: this is the only pilargid genus with branchiae, clearly indicating its monophyletic status.

*Glyphohesione* Friedrich, 1950: the opinion that this monotypic taxon should be included in *Ancistrosyllis* (ELIASON, 1962) or *Synelmis* (PETTIBONE, 1966) is rejected (see also FITZHUGH & WOLF, 1990, LICHER, in press) and the genus *Glyphohesione* should be retained. Specimens identified as *Synelmis klatti* (Friedrich, 1950) (six in the collection of the Zoologisk Museum Copenhagen (ZMUC) and one in the collection of the Senckenberg Museum Frankfurt (SMF)) differ from all pilargid taxa in possessing elongate, non-papilliform palpostyles and lateral antennae which are located near the anterior margin of the prostomium. They also do not possess emergent neuropodial spines which are characteristic for *Synelmis*. This is also true for two specimens from Florida in the collection of the U.S. National Museum Washington, although they differ slightly in other characters. The European and the American material both belong to *Glyphohesione* (LICHER, in press) (*Synelmis klatti* SMF 4432; ZMUC-POL-178; USNM 86986).

*Litocorsa* Pearson, 1970: the three species in this genus comprise a rather heterogeneous group in possessing three antennae, two antennae or none at all. Monophyly of the genus may be indicated by the presence of completely fused palps (FITZHUGH & WOLF, 1990).

*Parandalia* Emerson & Fauchald, 1971: the genus resembles *Loandalia* except that branchiae are absent. For the time being, however, no autapomorphic characters indicate its monophyly (*Parandalia ocularis*, collection of L. HARRIS, LACMNH; *P. tricuspis* USNM 123092).

*Paracabira* Britaev & Saphronova, 1981: tutapomorphies of the monotypic taxon are (1) lack of lateral antennae and (2) lack of dorsal parapodial cirri.

It cannot be completely discounted that *Loandalia, Parandalia* and *Talehsapia* do not belong to the Pilargidae at all. Because they almost or completely lack anterior appendages, their inclusion is mainly based on their comparatively simple parapodia with a stout notopodial spine. Thus their bearers could well be the endpoint of an evolutionary reductional series starting from another taxon within the Phyllodociformia (*sensu* FAUCHALD, 1977). (Omission of the three taxa from the analysis, however, would influence neither the cladistic results nor our reasoning about the phylogenetic origin of the Pilargidae.)

Despite SALAZAR-VALLEJO's (1986) argumentation, *Antonbruunia* Hartman & Boss, 1965, is not considered in our analysis. For the time being there is no convincing evidence for the pilargid nature of this monotypic taxon (see also FITZHUGH & WOLF, 1990). The recently erected Nautiliniellidae (MIURA & LAUBIER, 1989) have only superficial similarities to the pilargids.

OUTGROUP RELATIONSHIP. — Our phylogenetic analysis is based on the assumption that within the Pilargidae those taxa are the most primitive which possess (1) the highest number of head appendages (antennae, palps and tentacular cirri), (2) the best developed appendages, and (3) the highest number of chaetae and chaetal types. That is, an evolutionary pathway is hypothesized during which considerable reductions occurred, starting from taxa with three filiform antennae, two pairs of filiform tentacular cirri, biarticulated palps, and filiform dorsal parapodial cirri and leading to forms without any prostomial, tentacular and notopodial appendages (but see above). The general basis for this hypothesis is the idea that the stem species of the Phyllodociformia was richly equipped with head and body appendages which became differently and independently reduced within various taxa, especially in species with a totally endopsammic way of life.

By this line of argument *Sigambra* and *Glyphohesione* should be the most primitive pilargid taxa (LICHER, in press). Indeed, they show strong similarities with those small hesionid species which possess only a small number of body appendages. Similarities in number and arrangement of head appendages are obvious (Fig. 1). All the appendages in, e.g., a species of the genus *Hesionides* Friedrich, 1937 can be found in a *Sigambra* with the exception of the third tentacular cirri, which are still notopodial cirri of the first chaetigerous segment in *Sigambra*. The anterior-most ventral filiform appendages in *Hesionides* have a cirrus-like appearance. Investigations of their innervation, however, could prove them to be palps and therefore most likely homologous to the more fleshy and biarticulated palps in the pilargids [ultrastructural and immunohistochemical investigations by one of us (F. LICHER)].

For these interstitial hesionids a progenetic evolution has been considered (LAUBIER, 1967; WESTHEIDE, 1987b; WESTHEIDE & RIEGER, 1987); that is, it has been assumed that their speciation has taken place by genetically fixed maturation of juvenile stages of macrofaunal hesionid taxa. Now, we hypothesize that the pilargid stem species also evolved by progenesis of a larger hesionid's juvenile stage. The juvenile development of

Source : MNHN, Paris

non-interstitial hesionid species is characterized among other things by (1) a gradual increase in number of achaetous head segments, (2) an increase in the number of tentacular cirri, and (3) an expansion of articulation in the body appendages (HAALAND & SCHRAM, 1982, 1983) (Fig. 2). Adult hesionids belonging to different taxa especially differ in having different numbers of tentacular cirri - from three to eight pairs. Their youngest stage, e.g., an 8-chaetiger benthic stage of *Ophiodromus flexuosus* (Delle Chiaje, 1825) (corresponding to the earliest stage in the developmental series of Fig. 2) possesses the entire set of five prostomial appendages, but only one achaetous tentacular segment with two pairs of almost smooth cirri (HAALAND & SCHRAM, 1983). Thus its head morphology corresponds well with that of some pilargid taxa.

The idea that the pilargid stem species might have evolved by progenesis of a hesionid taxon caused us to use one of the hesionid taxa as the outgroup taxon for the data matrix of our cladogram (Table 2).

## METHODS

The phylogenetic analysis presented here was aided by the computer program HENNIG 86, version 1.5 (FARRIS, 1988). The program considers 14 taxa. We considered 28 morphological characters and 68 character states of which 40 are apomorphic (or 69 states, 41 apomorphic, see below) for the analysis (Table 1). Characters were compiled mainly from the various descriptions, including the characters of the brain study by FITZHUGH & WOLF (1990), and were complemented by our own observations. Multistate characters - that is, characters of more than one apomorphic state - were also used.

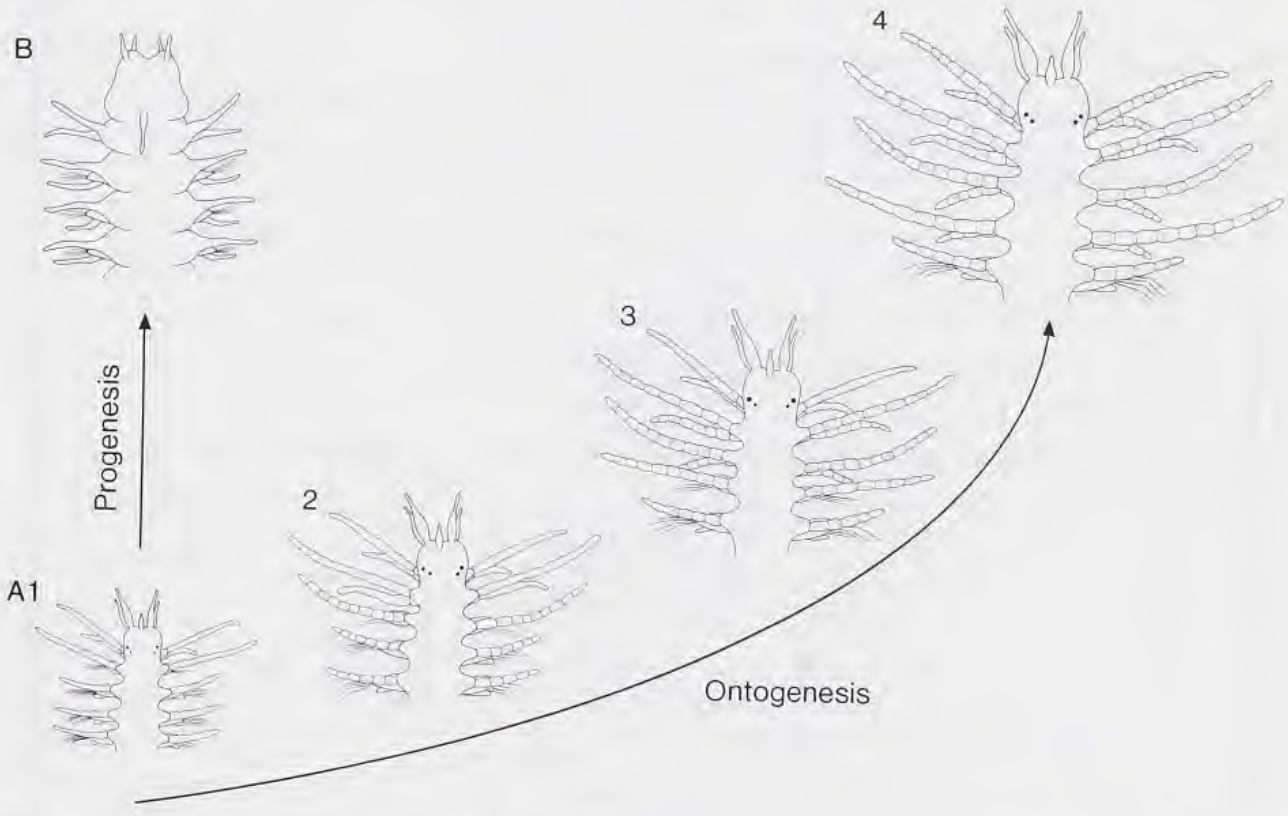



FIG. 2. — Schematic representation of progenetic origin of a primitive pilargid species from a hesionid juvenile stage: **a**, 1-4. Hesionid developmental series of a non-interstitial species, with (1) gradual increase in number of achaetous head segments, (2) a gradual increase in the number of tentacular cirri, and (3) an expansion of articulation in the cirral appendages, (see HAALAND & SCHRAM, 1983). — **b**, anterior end of a primitive pilargid taxon.

Source : MNHN, Paris

TABLE 1. — Characters and character states used in the phylogenetic analysis to set up the cladogram. Characters 10, 12, 17, 18, 22, 26 and 28 are multistate characters. Character 19 is coded twice belonging to different evolutionary ideas (see text for details). State "a" is plesiomorphic, subsequent states are apomorphic.

| Features | Character states | Coding |
|---|---|---|
| 1. Body-shape | a) Depressed | 0 |
| | b) Cylindrical | 1 |
| 2. Integument | a) Without papillae | 0 |
| | b) With papillae | 1 |
| 3. Anterior body region | a) Not inflated | 0 |
| | b) Inflated | 1 |
| 4. Prostomium | a) Wider than long or half rounded | 0 |
| | b) Longer than wide | 1 |
| 5. Prostomium | a) Clearly discernable | 0 |
| | b) Largely reduced | 1 |
| 6. Palps | a) Filiform, apparently not articulated | 0 |
| | b) Fleshy, well developed and biarticulated | 1 |
| 7. Palpostyles | a) Elongate | 0 |
| | b) Papillae-like | 1 |
| 8. Pharynx | a) Without jaws | 0 |
| | b) Jaws present | 1 |
| 9. Pharynx | a) Ring of papillae around the opening | 0 |
| | b) Without ring of papillae around the opening | 1 |
| 10. Antennae, lateral | a) Filiform and well developed | 0 |
| | b) Well developed, but shorter | 1 |
| | c) Almost reduced, papilla-like | 2 |
| | d) Missing | 3 |
| 11. Antennae, lateral | a) Located near the ant. margin of the prostomium | 0 |
| | b) Located posteriorly | 1 |
| 12. Antenna, median | a) Filiform and well developed | 0 |
| | b) Well developed, but shorter | 1 |
| | c) Almost reduced, papilla-like | 2 |
| | d) Missing | 3 |
| 13. Nuchal organ (Evaluation desired) | a) Present | 0 |
| | b) Missing | 1 |
| 14. Brain | a) About as long as wide | 0 |
| | b) Much longer than wide | 1 |
| 15. Brain divisions | a) Poorly divided | 0 |
| | b) Well divided | 1 |
| 16. Forebrain | a) Entire | 0 |
| | b) Bifurcate | 1 |
| 17. Hindbrain | a) With two lobes | 0 |
| | b) With three lobes | 1 |
| | c) With five lobes | 2 |
| 18. Tentacular cirri | a) Filiform and well developed | 0 |
| | b) Well developed, but shorter | 1 |
| | c) Almost reduced, papilla-like | 2 |
| | d) Missing | 3 |
| 19. I. Notopodia | a) Lacking | 0 |
| | b) With stout emergent hook | 1 |
| | c) With stout emergent spine | 2 |
| | d) Missing | 3 |
| 19. II. Notopodia | a) Lacking | 0 |
| | b) With stout emergent spine | 1 |
| | c) With stout emergent hook | 2 |
| 20. Notopodia | a) With capillary notochaetae besides spine or hook | 0 |
| | b) Further notochaetae missing | 1 |

Source : MNHN, Paris

| Features | Character states | Coding |
|---|---|---|
| 21. Notopodial aciculae | a) Present | 0 |
| | b) Missing | 1 |
| 22. Dorsal cirri | a) Filiform and well developed | 0 |
| | b) Well developed, but shorter | 1 |
| | c) Almost reduced, papilla-like | 2 |
| | d) Missing | 3 |
| 23. Dorsal cirri 1 | a) Longer than following ones | 0 |
| | b) Not longer than following ones | 1 |
| 24. Neuropodia | a) With compound chaetae | 0 |
| | b) Simple chaetae only | 1 |
| 25. Neuropodia | a) Distal ends of neurochaetae bifid | 0 |
| | b) Distal ends of neurochaetae pointed | 1 |
| 26. Neuropodia | a) Without emergent spines | 0 |
| | b) With two emergent spines, distally bifurcated | 1 |
| | c) With two emergent spines, distally pointed | 2 |
| 27. Ventral cirri 1 | a) Present | 0 |
| | b) Missing | 1 |
| 28. Anal cirri, lateral | a) Filiform and well developed | 0 |
| | b) Well developed, but shorter | 1 |
| | c) Almost reduced, papilla-like | 2 |
| | d) Missing | 3 |

As it is difficult to decide whether the notopodial hook or the notopodial straight spine is the more apomorphic character state (considering hooks and spines as homologous) we constructed two data matrices to accommodate the following different ideas (but see LICHER, in press): (1) The hook is plesiomorphic and already present in the

TABLE 2. — Data matrix of 14 taxa and 28 characters used in the phylogenetic analysis. Outgroup is *Hesionides* Friedrich, 1937. Character numbers and character states as in Table 1. Character 19 is subdivided belonging to different evolutionary ideas (see text for details). Cases in which the state is unknown or questionable are indicated as "?", cases in which the character is not present are indicated as "-".

| | 12345 | 1 67890 | 11111 12345 I II | 111 12 67890 | 22222 12345 | 222 678 |
|---|---|---|---|---|---|---|
| *Hesionides* | 00000 | 00000 | 00?00 | 0?0000 | 00000 | 000 |
| *Ancistrosyllis* | 00100 | 11001 | ?1000 | 021121 | 01010 | 001 |
| *Cabira* | ?0100 | 11102 | 13000 | 012121 | 02110 | 013 |
| *Glyphohesione* | 00000 | 100?0 | 00000 | 000211 | 00111 | 000 |
| *Litocorsa* | 1?010 | 1011 | ?1111 | 001211 | 01111 | 2?1 |
| *Loandalia* | 11001 | 11013 | -3011 | 103210 | 13111 | 012 |
| *Otopsis* | 00000 | 11001 | 11??? | ??130? | 01110 | 01? |
| *Paracabira* | ?010? | 110?3 | -3?00 | 012121 | 03110 | 00? |
| *Parandalia* | 11001 | 11013 | -3011 | 103210 | 13111 | 0?2 |
| *Parandalia* | 11001 | 11013 | -3011 | 103210 | 13111 | 0?2 |
| *Pilargis* | 00100 | 110?1 | 13010 | 011301 | 01010 | 001 |
| *Sigambra* | 00000 | 11000 | 10000 | 00012? | 00011 | 000 |
| *Synelmis* complex A | 10000 | 11011 | 11111 | 101211 | 01111 | 101 |
| *Synelmis* complex B | 10010 | 110?1 | ?1111 | 101211 | 01111 | 201 |
| *Talehsapia* | 11001 | --1?3 | -3??? | ??3211 | 1311? | 002 |

Source : MNHN, Paris

stem species of the Pilargidae; the spine is apomorphic and derived from a hook by simplification; the absence of hooks and spines is secondary, possibly reduced several times. (2) Lack of hooks or spines is plesiomorphic; a spine is apomorphic and evolved from a simple notochaeta within the Pilargidae; a hook is more apomorphic and derived from a spine, possibly derived several times (see FITZHUGH & WOLF 1990). Both ideas are reflected in our data matrix (Table 2): character 19 (I) corresponds to the first idea, character 19 (II) to the second one.

The cladogram was constructed from the data matrix using the ie* command. This command generates cladograms by implicit enumeration, producing all possible minimum-length cladograms. Successive character weighting was carried out using the xs - w command. Computer runs were made on an IBM-compatible 486 DX, 33 MHz computer.

## RESULTS

Considering the notopodial hook to be the plesiomorphic character state (coding I for character 19) only a single cladogram is produced (Fig. 3a). The length is 63 steps, consistency index (c.i.) is 0.66, retention index (r.i.) is 0.79. An analysis that considers the notopodial hook to be the most apomorphic state (coding II for character 19) yielded two cladograms, one of which is the same as in coding I (Figs 3a-b). The lengths of the two cladograms are 63 steps (c.i. 0.65, r.i. 0.78). Successive character weigthing yielded one minimum-length tree (Fig. 3b).

The results of both codings are nearly the same: *Glyphohesione* is the adelphotaxon of all other pilargids, of which *Sigambra* is the sister-group of the remaining 11 taxa. The latter genera are arranged in two groups and *Otopsis*: (1) *Ancistrosyllis*, *Pilargis*, *Cabira* and *Paracabira*, and (2) the two *Synelmis*-complexes, *Litocorsa*, *Talehsapia*, *Parandalia* and *Loandalia*. In both cladograms the relationships are identical with the exception of *Otopsis* (see Figs 3a-b).

The two cladograms show *Glyphohesione* to be the pilargid with the highest number of plesiomorphic characters (e.g., elongate palpostyles, lateral antennae located at the anterior margin of the prostomium). All other pilargids bear papilla-like palpostyles (state 7b, Table 1 and Fig. 4) and lateral antennae located posteriorly (11b). *Glyphohesione* is characterized by three autapomorphies (19c, 23b, 25b, using coding I) or by two autapomorphies (19c, 23b, using coding II). The monophyly of *Sigambra* is questionable when the notopodial hook is considered to be plesiomorphic (coding I).

The *Ancistrosyllis*-group, *Otopsis* and the *Synelmis*-group possess prostomial, tentacular, parapodial and anal appendages (10b, 12b, 18b, 22b, 28b), which are shorter than in *Glyphohesione* and *Sigambra*. The *Ancistrosyllis*-group is clearly characterized by the possession of a papillated integument (2b) and a three-lobed hindbrain (17b). Using coding II the possession of a dorsal hook would be an additional synapomorphy. *Ancistrosyllis* may be characterized by its five-lobed hindbrain (17c), whereas the stem-species of *Pilargis*, *Cabira* and *Paracabira* lost the median antenna (12d). Autapomorphies of *Pilargis* are the loss of notopodial hooks (19d - reversion) and the possession of a brain which is much longer than wide (14b). In the stem-species of *Cabira* and *Paracabira* further reductions occurred (10c, 18c, 22c, 23b). *Cabira* bears jaws (8b) and lacks ventral cirri on chaetiger 1 as well as anal cirri (27b, 28d). *Paracabira* lacks lateral antennae and dorsal cirri (10d, 22d).

*Otopsis* and the *Synelmis*-group are equipped with dorsal cirri on chaetigerous segment 1, which are not longer than the following ones (23b). *Otopsis* is characterized by two reductions (19d, 27b). The *Synelmis*-group possesses a series of synapomorphic features: a cylindrical body (1b), a pharynx without distal papillae (9b), only simple capillary neurochaetae (25b), and several characters of brain gross morphology considered to be characteristic for them by FITZHUGH & WOLF (1990) (14b, 15b, 16b). Possession of a notopodial spine (19c) is an additional synapomorphy of this taxon when the hook is considered to be the plesiomorphic character state.

The two *Synelmis* complexes and *Litocorsa* possess two emergent neuropodial spines (26b) and lack nuchal organs (13b) according to FITZHUGH & WOLF (1990). The *Synelmis*-species (= *Synelmis* complex A plus *Synelmis* complex B) can be shown to form a paraphyletic group. Synapomorphies for *Synelmis* complex B and *Litocorsa* are the possession of pointed neuropodial spines (26c) and possession of a prostomium which is somewhat longer than wide (4b). Autapomorphies for *Litocorsa* are an "entire" forebrain (16a - reversion) and fused palps. Presence of prostomial pigmented eyes may be the autapomorphy of *Synelmis* complex A. For the time being no autapomorphies exist for *Synelmis* complex B.

*Talehsapia*, *Parandalia* and *Loandalia* show several synapomorphies: an inflated anterior body region (3b), a largely reduced prostomium (5b), loss of lateral and median antennae, tentacular cirri and dorsal cirri (10d, 12d, 18d, 22d), loss of notopodial aciculae (21b), loss of ventral cirri on chaetiger 1 (27b), and possession of papilla-

Source : MNHN, Paris

like anal cirri (28c). *Talehsapia* is characterized by the possession of jaws (8b). The notopodia of *Loandalia* and *Parandalia* are equipped with simple capillary notochaetae accompanying the stout spine (20a - reversion). *Loandalia* is unique in possessing branchiae and has lost the ventral cirri in chaetiger 1 (27b). Monophyly of *Parandalia* is questionable.

## DISCUSSION

OUTGROUP RELATIONSHIP. — FITZHUGH & WOLF (1990) recognized either the Syllidae-Hesionidae-Nereididae complex or the Syllidae alone as possible outgroups of the Pilargidae. Whereas the relationship of the Pilargidae to the Nereidiformia is evident, a syllid-pilargid sister-group relationship based only on the presence of simple neurochaetae with bifid distal ends, however, appears to us less probable.

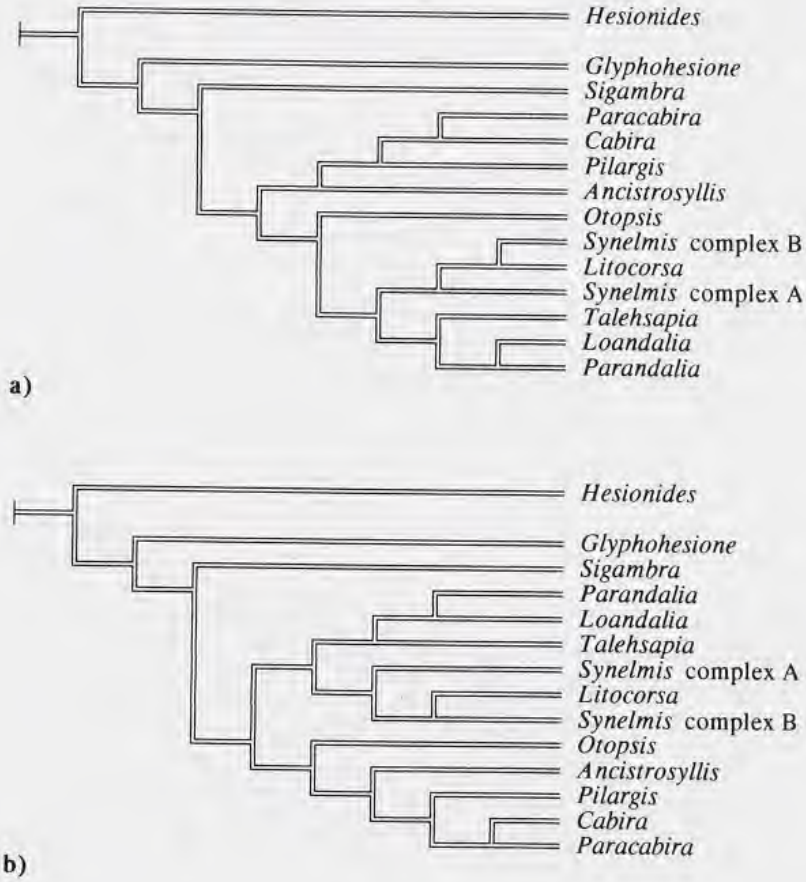



FIG. 3. — Cladograms of pilargid genera using different codings for character 19: **a**, the only cladogram produced using coding I. — **b**, the retained cladogram after successive character weighting using coding II (see text for details).

A possible nereidid-pilargid relationship was mentioned, e.g., by GLASBY (1990). A pilargid progenetic evolution of nereidid macroforms appears also conceivable, since nereidids possess a juvenile stage with two pairs of tentacular cirri (HAUENSCHILD & FISCHER, 1969, Fig. 8) which resembles primitive pilargid taxa (e.g., *Sigambra*). The nereidid juveniles, however, possess jaws, and lack a median antenna.

We, therefore, strongly support the Hesionidae as closest relatives of the Pilargidae. There is not only the high similarity between juvenile hesionids and primitive pilargid taxa; both taxa also generally coincide in the

Source : MNHN, Paris

morphology of head, parapodia and pharynx. The genus *Hesionides* is only slightly less reduced than primitive pilargids in possessing two tentacular segments and three tentacular cirri (see Fig. 1). However, the probability of an independent progenetic evolution of both *Hesionides* and the pilargid stem species cannot be excluded.

The largest differences between Hesionidae and Pilargidae were hitherto seen in their chaetation: pilargids with their acicula-like stout notopodial hooks or spines and exclusively simple neurochaetae versus hesionids with mostly capillary notochaetae and a neuropodial chaetation which always includes compound chaetae. Chaetation in the two taxa, however, may be less different than formerly supposed: (1) Spines and hooks are not homologous to aciculae, but derived notochaetae, which in some cases occur together with a true acicula (as FITZHUGH & WOLF, 1990 pointed out). (2) Just recently two hesionid species have been found with apparent pilargid chaetal features. *Microphthalmus simplicichaetosus* Westheide & Purschke, 1992, has exclusively simple bidentate neurochaetae. An undescribed *Microphthalmus* (WESTHEIDE, in prep.) is equipped with typical notopodial hooks. HARTMANN-SCHRÖDER (1962) described a *Microphthalmus ancistrosyllïiformis* [sic!] because of its conspicuous notopodial spines. A strong notopodial spine is also present in *Hesiospina* Imajima & Hartman, 1964. Without doubt none of these species can be used as a sister-group for the Pilargidae. They demonstrate, however, that potential tendencies toward pilargid chaetation exist in hesionid taxa.

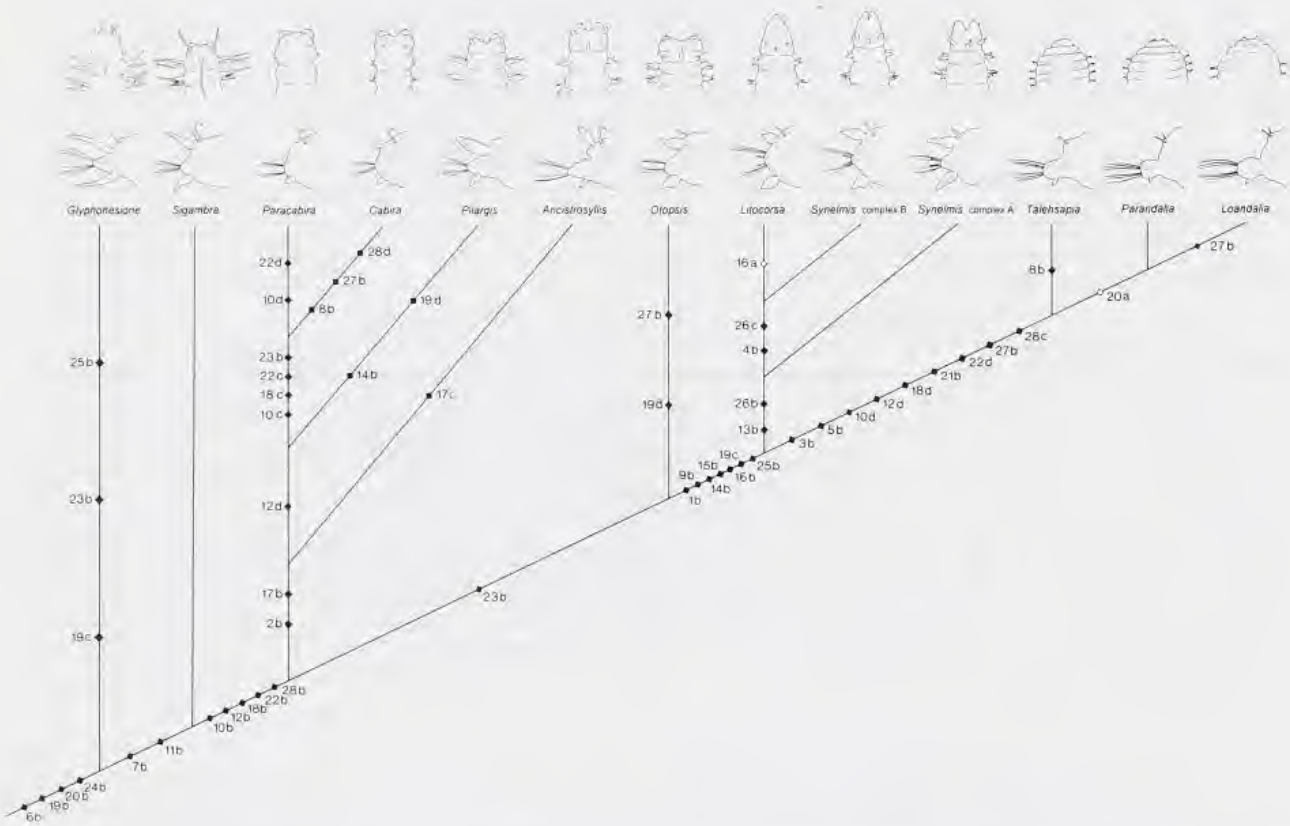



FIG. 4. — Cladogram of pilargid genera together with the outlines of anterior ends and parapodia. The outgroup is *Hesionides* Friedrich, 1937. Solid rhombs represent apomorphies, open rhombs symbolize character reversals. Numbers refer to characters in Table 1.

Unfortunately, most of the hesionid-pilargid similarities may be considered to be plesiomorphic characters going back to the stem species of the Nereidiformia. The autapomorphic character for the Hesionidae with the

Source : MNHN, Paris

strongest probability may be a large number of tentacular cirri (eight pairs), which, however, is not present in the hesionid juvenile stages (see above). Thus, even species assumed to be evolved from hesionid juveniles - the pilargid stem species in our opinion - cannot possess this character. This renders it extremely difficult to demonstrate a synapomorphy for Hesionidae and Pilargidae.

RELATIONSHIPS WITHIN THE PILARGIDAE. — There is no evidence that a division of the Pilargidae into Synelminae and "Sigambrinae" (SALAZAR-VALLEJO, 1986, 1990, SALAZAR-VALLEJO & SOLÍS-WEISS, 1992), or Synelminae and "Pilarginae" (SALAZAR-VALLEJO & ORENSANZ, 1991) is justified (see also FITZHUGH & WOLF, 1990). The "Sigambrinae" (="Pilarginae") consisting of *Sigambra*, *Ancistrosyllis*, *Ancistargis*, *Pilargis*, *Cabira* and *Paracabira* are not based on any apomorphic feature.

Considering the absence of a notopodial hook in *Pilargis* and *Otopsis* to be a loss is more probable than to be the plesiomorphic state. In the latter case one must assume that a notopodial hook was independently evolved three times: in *Sigambra*, in *Ancistrosyllis*, and in the stem-species of *Cabira* and *Paracabira*. Therefore, *Otopsis* is likely the adelphotaxon of the *Synelmis*-group (Fig. 4).

The species of *Litocorsa* and *Synelmis* complex B are closely related (Fig. 4). Since no autapomorphies for the latter could be found, inclusion of them in *Litocorsa* is proposed. This taxon then contains the following species:

*Litocorsa annamita* (Gallardo, 1967),
*Litocorsa stremma* Pearson, 1970,
*Litocorsa dineti* (Katzmann, Laubier & Ramos, 1974),
*Litocorsa acuminata* (Wolf, 1986),
*Litocorsa antennata* Wolf, 1986,
*Litocorsa ewingi* (Wolf, 1986),
*Litocorsa dentata* Imajima, 1987.

The diagnosis of the genus *Litocorsa* thus must be emended and reads as follows: "Body cylindrical. Prostomium longer than wide, with two, three or without antennae. Palps incompletely or totally fused. Two pairs of short tentacular cirri. Notopodial emergent spine present, neuropodia with two stout non-furcate spines besides capillary ones. Pygidium with two short anal cirri."

*Synelmis* (= *Synelmis* complex A) differs from *Litocorsa* (= *Litocorsa* plus *Synelmis* complex B) in always possessing three antennae, pigmented prostomial eyes and neuropodia with two stout furcate spines; it includes the following species:

*Synelmis albini* (Langerhans, 1881),
*Synelmis simplex* Chamberlin, 1919.

Also for *Parandalia* no autapomorphies are obvious. Inclusion of the *Parandalia*-species in *Loandalia*, however, is not suggested. Some *Parandalia*-species show closer similiarities (synapomorphies?) to *Loandalia* (absence of ventral cirri on chaetiger 1 (27b) in *P. tricuspis* (Müller, 1858), *P. ocularis* Emerson & Fauchald, 1971, *P. vivianneae* Salazar-Vallejo, 1990; possession of a median anal cirrus in *P. indica* (Thomas, 1963), *P. ocularis* Emerson & Fauchald, 1971 and *P. bennei* Solís-Weiss, 1983).

Given that the pilargids evolved progenetically from a larger hesionid species, it follows that the Hesionidae are a paraphyletic taxon if the Pilargidae are kept as an independent family. Phylogenetic systematic implications consequently require that the Pilargidae be included in the Hesionidae and not be considered an independent family. This suggestion is not so new at all; especially FAUVEL (1919a, 1919b, 1920, 1923, 1932), but also EHLERS (1908), HORST (1921), SOUTHERN (1921), AUGENER (1927), MONRO (1933), MESNIL & FAUVEL (1939), BERKELEY & BERKELEY (1941) and TREADWELL (1941) positioned pilargid species in the taxon Hesionidae. The phylogenetic systematical partitioning within such an enlarged family Hesionidae to create, e.g., subfamilies must be reserved till a comprehensive revision has been made of the "true" hesionid taxa.

## ACKNOWLEDGEMENTS

We are indebted to Prof. Dr. K. FAUCHALD, Smithsonian Institution Washington (USNM), Dr. M.E. PETERSEN, Zoological Museum, University of Copenhagen (ZMUC), L.H. HARRIS, Los Angeles County Museum of Natural History (LACMNH), Dr. D. FIEGE, Senckenberg Museum Frankfurt (SMF), and A. NATEEWATHANA, Phuket Marine Biological Center, Thailand for the friendly loan of pilargid species. Special thanks are due to Dr.

Source : MNHN, Paris

D. EIBYE-JACOBSEN, (ZMUC) for his helpful advice in using HENNIG 86. Many ideas and comments he provided have been of considerable help in setting up our cladograms.

## REFERENCES

AUGENER, H., 1927. — Polychaeten von Südost- und Süd-Australien. *Vidensk. Meddr dansk naturh. Foren*, **83** : 71-275.

BERKELEY, E. & BERKELEY, C., 1941. — On a collection of Polychaeta from Southern California. *Bull. South. Calif. Acad. Sci.*, **40** : 16-60.

BRITAEV, T.A. & SAPHRONOVA, M.A., 1981. — New species of the family Pilargidae (Polychaeta) from the Sea of Japan and revision of the genus *Cabira*. *Zool. Zhur.*, **60** : 1314-1324. [In Russian, English summary]

EHLERS, E., 1908. — Die bodensässigen Anneliden aus den Sammlungen der Deutschen Tiefsee-Expedition. *Wiss. Ergeb. Deutschen Tiefsee-Exped.* 1897-1899, **16** : 1-168.

ELIASON, A., 1962. — Undersökningar över Öresund, 41: Weitere Untersuchungen über die Polychaetenfauna des Öresunds. *Lunds Univ. Arsskr.*, n.f., **58** : 1-97.

EMERSON, R.R. & FAUCHALD, K., 1971. — A revision of the genus *Loandalia* Monro with description of a new genus and species of pilargiid polychaete. *Bull. South. Calif. Acad. Sci.*, **70** : 18-22.

FARRIS, J.S., 1988. — *Hennig 86 reference, version 1.5*. New York, 41 Admiral Street, Port Jefferson Station 11776, 17 pp.

FAUCHALD, K., 1977. — *The polychaete worms. Definitions and keys to the orders, families and genera*. Nat. Hist. Mus. Los Angeles County, California, **28** : 1-190.

FAUVEL, P., 1919a. — Annélides Polychètes des îles Gambier et Touamotou. *Bull. Mus. natl Hist. nat., Paris*, **25** : 336-343.

FAUVEL, P., 1919b. — Annélides Polychètes de Madagascar, de Djibouti et du Golfe Persique. *Zool. Exp. Gén., Paris*, **58** : 315-473.

FAUVEL, P., 1920. — Les genres *Ancistrosyllis* et *Pilargis* (Hesionidae). *Bull. Soc. Zool. Fr.*, **45** : 205-213.

FAUVEL, P., 1923. — Polychètes Érrantes. *Faune Fr.*, **5**: 1-488.

FAUVEL, P., 1932. — Annelida Polychaeta of the Indian Museum, Calcutta. *Mem. Indian Mus., Calcutta*, **12** : 1-262.

FITZHUGH, K. & WOLF, P.S., 1990. — Gross morphology of the brain of pilargid polychaetes: Taxonomic and systematic implications. *Amer. Mus. Nov.*, **10024** (2992) : 1-16.

FRIEDRICH, H., 1937. — Polychaetenstudien I - III. *Kieler Meeresforsch.*, **1** : 343-345.

GARDINER, S.L., 1976. — Errant polychaete annelids from North Carolina. *J. Elisha Mitchell Sci. Soc.*, **91** : 77-220.

GLASBY, C.J., 1990. — Phylogenetic relationships in the Nereididae (Annelida: Polychaeta), chiefly in the subfamily Gymnonereidinae, and the monophyly of the Namanereidinae. *Bull. Mar. Sci.*, **48** : 559-573.

HAALAND, B. & SCHRAM, T.A., 1982. — Larval development and metamorphosis of *Gyptis rosea* (Hesionidae, Polychaeta). *Sarsia*, **67** : 107-118.

HAALAND, B. & SCHRAM, T.A., 1983. — Larval development and metamorphosis of *Ophidromus flexuosus* (Delle Chiaje) (Hesionidae, Polychaeta). *Sarsia, Bergen*, **68** : 85-96.

HARTMAN, O., 1959. — Catalogue of the polychaetous annelids of the world. Part 1, 2. *Allan Hancock Found. Publ. Occ. Pap.*, **23** : 1-628.

HARTMANN-SCHRÖDER, G., 1962. — Zur Kenntnis des Eulitorals der chilenischen Pazifikküste und der argentinischen Küste Südpatagoniens unter besonderer Berücksichtigung der Polychaeten und Ostracoden. II. Die Polychaeten des Eulitorals. *Mitt. Hamb. Zool. Mus. Inst.*, Ergänzungsband zu **60** : 57-167.

HAUENSCHILD, C. & FISCHER, A., 1969. — *Platynereis dumerilii. Mikroskopische Anatomie, Fortpflanzung, Entwicklung*. Großes Zoologisches Praktikum, Fischer, Stuttgart, Heft **9b** : 1-55.

HESSLE, C., 1925. — Einiges über die Hesioniden und die Stellung der Gattung *Ancistrosyllis*. *Ark. Zool. Stockholm*, **17a** : 1-36.

HORST, R., 1921. — A review of the family of Hesionidae with a description of two new species. *Zool. Meded., Leyden*, **6** : 73-83.

Source : MNHN, Paris

IMAJIMA, M. & HARTMAN, O., 1964. — The polychaetous annelids of Japan, pt. 1. *Allan Hancock Found. Publ. Occ. Pap.*, **26** : 1-237.

JONES, M.L., 1961. — Two new polychaetes of the families Pilargidae and Capitellidae from the Gulf of Mexico. *Amer. Mus. Nov.*, **2049** : 1-18.

LAUBIER, L., 1967. — Adaptations chez les Annélides Polychètes interstitielles. *Ann. Biol.*, **6** : 1-16.

MESNIL, F. & FAUVEL, P., 1939. — Polychètes sédentaires de l'expédition du Siboga: Maldanidae, Cirratulidae, Capitellidae, Sabellidae et Serpulidae. *Siboga-Expedition*, **24** : 1-42.

MIURA, T. & LAUBIER, L., 1989. — *Nautilina calyptogenicola*, a new genus and species of parasitic polychaete on a vesicomyid bivalve from the Japan Trench, representative of a new family Nautiliniellidae. *Zool. Sci., Japan*, **6** : 387-390.

MONRO, C.C.A., 1933. — On a new species of Polychaeta of the genus *Pilargis* from Friday Harbour, Washington. *Ann. Mag. Nat. Hist.*, **10** (11) : 673-675.

PETTIBONE, M.H., 1966. — Revision of the Pilargidae (Annelida: Polychaeta), including descriptions of new species, and redescriptions of the pelagic *Podarmus ploa* Chamberlin (Polynoidae). *Proc. U.S. Nat. Mus.*, **118** (3525) : 155-208.

SAINT-JOSEPH, A. de, 1899. — Note sur une nouvelle famille d'Annélides Polychètes (Pilargidiens). *Bull. Mus. Hist. nat., Paris*, **5** : 41-42.

SALAZAR-VALLEJO, S.I., 1986. — Pilargidae (Annelida: Polychaeta) de Mexico: Lista de especies, nueva especie y biografia. *Cah. Biol. mar.*, **27** : 193-209.

SALAZAR-VALLEJO, S.I., 1990. — Redescriptions of *Sigambra grubii* Müller, 1858 and *Hermundura tricuspis* Müller, 1858 from Brazil and designation of neotypes (Polychaeta: Pilargidae). *J. Nat. Hist.*, **24** : 507-517.

SALAZAR-VALLEJO, S.I. & ORENSANZ, J.M., 1991. — Pilárgidos (Annelida: Polychaeta) de Uruguay y Argentina. *Cah. Biol. mar.*, **32** : 267-279.

SALAZAR-VALLEJO, S.I. & SOLÍS-WEISS, V., 1992. — Biogeography of the pilargid polychaetes (Polychaeta Pilargidae) of the subfamily Synelminae. In: S.P. DARWIN & A.L. WELDEN (eds.), Biogeography of Mesoamerica. Proceedings of a Symposium, Mérida, México, Oct. 1984. *Tulane Stud. Zool. Bot.*, Suppl. Publ. 1.

SOUTHERN, R., 1921. — Fauna of the Chilka Lake. Polychaeta of the Chilka Lake and also of fresh and brackish waters in other parts of India. *Mem. Ind. Mus.*, **5** : 565-660.

TREADWELL, A.L., 1941. — Polychaetous annelids from the New England region, Porto Rico and Brazil. *Amer. Mus. Nov.*, **1138** : 1-4.

WESTHEIDE, W., 1967. — Monographie der Gattungen *Hesionides* Friedrich und *Microphthalmus* Mecznikow (Polychaeta, Hesionidae). II. Zoologisches Institut und Museum der Universität Göttingen. *Z. Morph. Tiere*, **61** : 1-159

WESTHEIDE, W., 1987a. — The interstitial polychaete *Hesionides pettiboneae* n.sp. (Hesionidae) from U.S. east coast and its transatlantic relationship. *Bull. biol. Soc., Wash.*, **7** : 131-139.

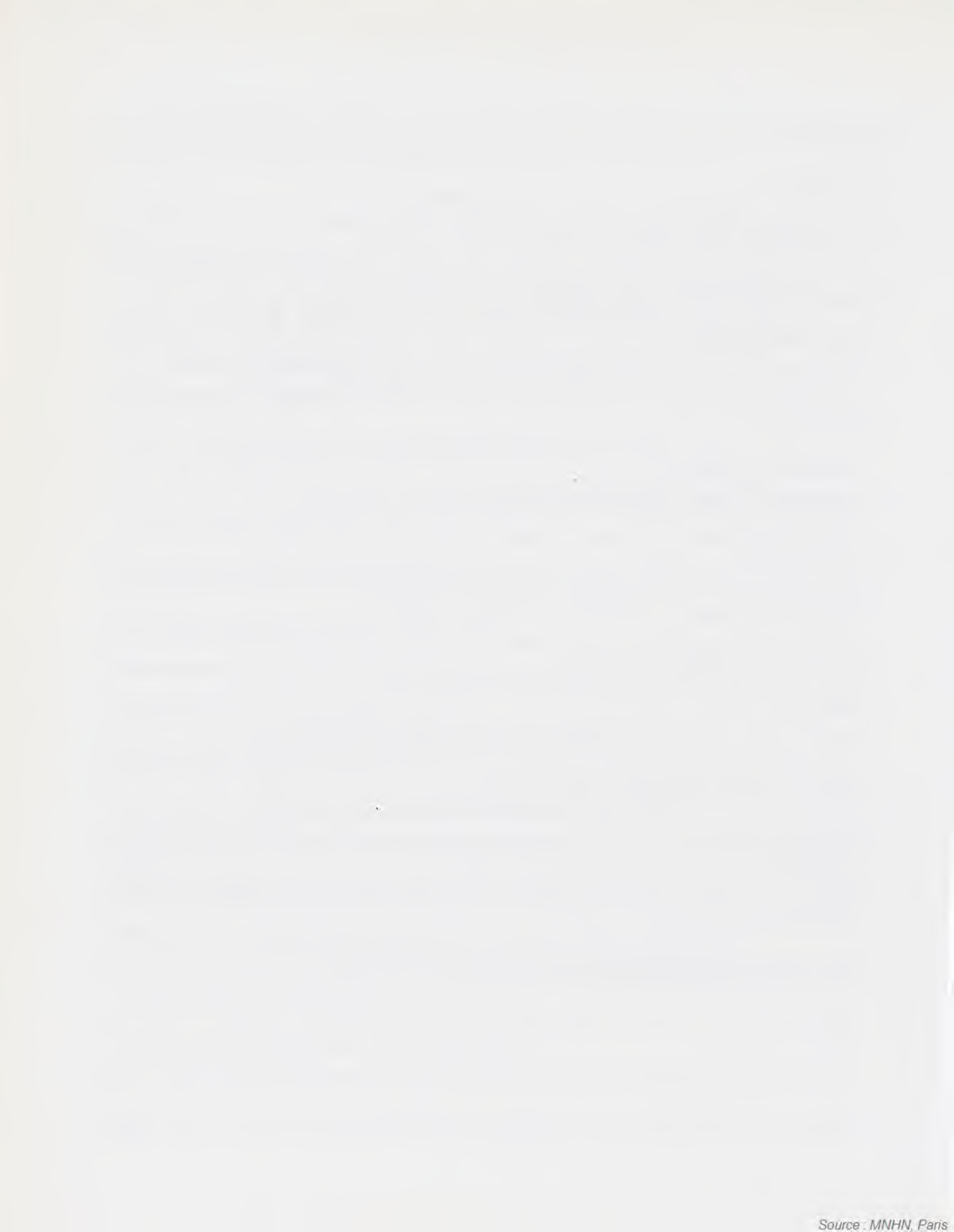
WESTHEIDE, W., 1987b. — Progenesis as a principle in meiofauna evolution. *J. nat. Hist.*, **21** : 843-854.

WESTHEIDE, W. & PURSCHKE, G., 1992. — *Microphthalmus simplicichaetosus* (Annelida: Polychaeta), a new hesionid from the Northwestern American Pacific Coast with exclusively simple chaetae. *Proc. Biol. Soc., Wash.*, **105** (1) : 132-135.

WESTHEIDE, W. & RIEGER, R.M., 1987. — Systematics of the amphiatlantic *Microphthalmus-listensis* species-group (Polychaeta: Hesionidae): facts and concepts for reconstruction of phylogeny and speciation. *Z. zool. Syst. Evolutionsforsch.*, **25** : 12-39.

WOLF, P.S., 1984. — Family Pilargidae Saint-Joseph, 1899. *In*: J.M. UEBELACKER & P.G. JOHNSON (eds), *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico*, **7** (4). Barry A. VITTOR & Ass., Mobile, **29** : 1-41.

Source : MNHN, Paris



Source : MNHN, Paris

# *Pseudatherospio fauchaldi*, a new genus and species of Spionidae (Polychaeta, Annelida) from southern California, USA

*Lawrence L. LOVELL*

1036 Buena Vista Drive, Vista
California 92083-7411, USA

ABSTRACT

*Pseudatherospio fauchaldi*, a new genus and species of Spionidae is described from material collected from a depth of 197 m off Huntington Beach, southern California. The main characteristics of the genus are the distribution and shape of branchiae, the presence of fringed neuropodial setae in anterior setigers and the structure of modified neuropodial hooks in posterior setigers. Generic affinities are discussed. *Pseudatherospio* most closely resembles *Atherospio* Mackie & Duff, 1986 and *Pygospiopsis* Blake, 1983.

RÉSUMÉ

***Pseudatherospio fauchaldi*, genre et espèce nouveaux de Spionidae (Annélides, Polychètes) de Californie du Sud**

*Pseudatherospio fauchaldi*, genre et espèce nouveaux de Spionidae est décrit à partir de matériel récolté par 197 m de profondeur au large d'Huntington Beach, Californie du sud. La distribution et la forme des branchies présentes dès le premier sétigère, la présence de soies neuropodiales frangées aux sétigères antérieurs et la structure des crochets modifiés des sétigères postérieurs dont la dent secondaire est située au-dessous de la dent principale du côté concave du crochet sont les caractéristiques essentielles du genre. Les affinités génériques avec les genres les plus proches, *Atherospio* Mackie & Duff, 1986 and *Pygospiopsis* Blake, 1983 sont discutées.

## INTRODUCTION

A new genus and species of Spionidae is described from a sample collected at a depth of 197 m off Huntington Beach, southern California, during July 1991. Specimens were collected by MEC Analytical Systems, Inc. (contract number 02091) as part of the E.P.A. 301(h) waste water outfall monitoring program of the County Sanitation Districts of Orange County (CSDOC).

Type material has been deposited in the following museums: Allan Hancock Foundation Polychaete Collection

LOVELL, L.L., 1994. — *Pseudatherospio fauchaldi*, a new genus and species of Spionidae (Polychaeta, Annelida) from Southern California, USA. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 237-241. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

of the Los Angeles County Museum of Natural History, Los Angeles, California (LACM-AHF) and National Museum of Natural History, Washington, D.C. (USNM).

## SYSTEMATICS

### *Pseudatherospio* gen. nov.

**Type species**. — *Pseudatherospio fauchaldi* sp. nov. Gender, feminine.

**Diagnosis**. — Prostomium longer than wide, anterior margin bilobed, tapering posteriorly; eyes absent; occipital tentacle present. Branchiae from setiger 1 to at least setiger 36; outer margin fused with notopodial lamellae on setigers 7-15 or 16, free otherwise; terminate with short, digitate process. Interramal 'genital' pouches absent. Setigers 2-16 with dorsal intrasegmental and intersegmental ciliary bands. Parapodia biramous. Notosetae capillary. Neurosetae include capillary setae; fringed setae; bidentate, strongly-curved, hooded hooks. Sabre setae absent. Pygidium unknown.

**Etymology**. — The generic name refers to the close resemblance to *Atherospio* Mackie & Duff, 1986.

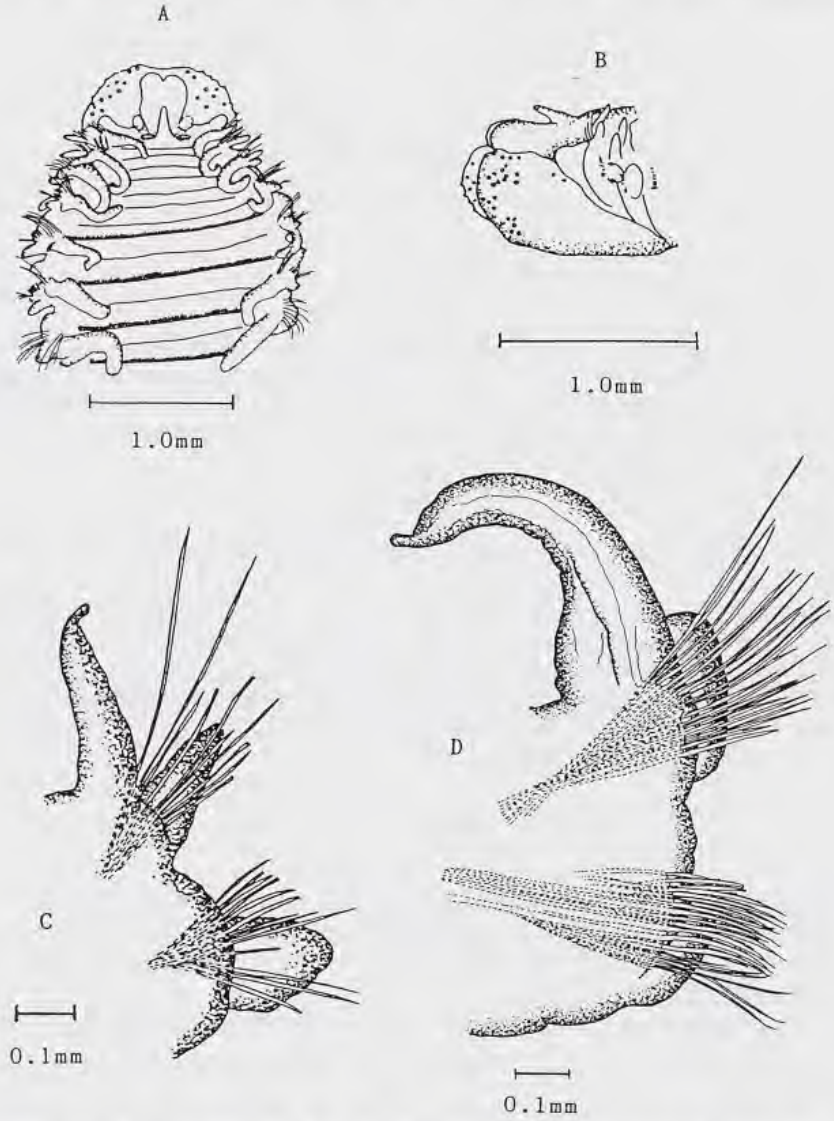



FIG. 1. — *Pseudatherospio fauchaldi* gen. sp. nov. A, Anterior end, dorsal view. B, Anterior end, lateral view. C, Parapodium from setiger 1, anterior view. D, Parapodium from setiger 5, anterior view.

Source : MNHN, Paris

## *Pseudatherospio fauchaldi* sp. nov.

(Figs 1 & 2)

**Material.** — Pacific Ocean, Southern California, R. V. CRUSADER; collector: C. FULLER, station 25, 33°33'48"N, 118°02'11"W, 197 m, green mud, 24 July 1991, holotype (LACMNH-AHF1650), 1 paratype (LACM-AHF1651) and 1 paratype (USNM163804).

**Description.** — Holotype incomplete, with 36 setigers; total length 9.5 mm; width 0.8 mm (excluding parapodial lobes) at setiger 1, 1.3 mm at setiger 6. Paratypes incomplete, each with 22 setigers; total length 6.7 mm and 9.6 mm, respectively; width 0.8 and 1.8 mm at setiger 1, and 1.9 and 3.7 mm at setiger 6, respectively.

Prostomium longer than wide, anterior margin bilobed, tapering posteriorly to setiger 1; eyes absent; occipital tentacle short, distally tapering, emerging from anterior margin of setiger 1 (Fig. 1A-B). Pair of grooved palps inserted on peristomium near postero-lateral margins of prostomium, extending to setiger 12. Peristomium poorly developed, only visable along postero-lateral margin of prostomium, remainder fused to setiger 1. Small, transverse nuchal organs present behind palps at anterior margin of setiger 1. Everted proboscis delicate, translucent sac with medial groove and low, conical papillae on the fronto-lateral margin (Fig. 1A-B).

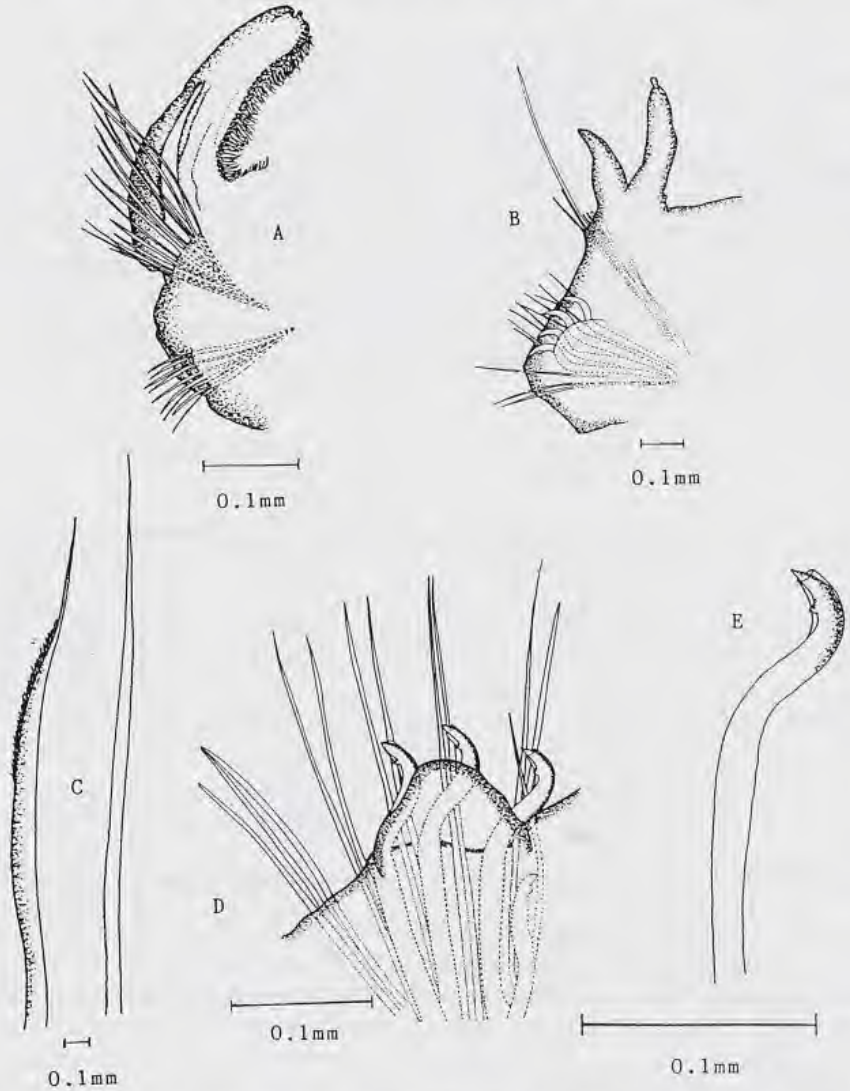



FIG. 2. — *Pseudatherospio fauchaldi* gen. sp. nov. A, Parapodium from setiger 9, anterior view. B, Parapodium from setiger 26, posterior view. C, Fringed seta and capillary seta from setiger 5. D, Neuropodial ramous from setiger 20. E, Neuropodial hooded hook from setiger 20.

Source : MNHN, Paris

Parapodia biramous. Notopodial postsetal lamellae long, triangular on setiger 1 (Fig. 1C); shorter and more broad by setiger 5 (Fig. 1D); completely fused with outer branchial margin on setigers 7-15 or 16 (Fig. 2A); long, triangular after setiger 15 or 16 (Fig. 2B). Neuropodial postsetal lamellae broadly triangular on setiger 1 (Fig. 1C); shorter and more broad by setiger 5 (Fig. 1D); a low mound on setigers 7-15 or 16 (Fig. 2A); lamellae short, broadly triangular after setiger 16 or 17 (Fig. 2D). Ventral scutes or pads absent.

Branchiae begin on setiger 1, on all setigers present. Branchiae cirriform and free from notopodial lamellae on setigers 1-6 and15 or 16-36 (Figs 1C-D, 2B); branchiae fused to lamellae on setigers 7-14 or 15, with inner lateral margins densely ciliated (Fig. 2A). Branchiae terminate with a short, narrow, digitate process; greatly reduced in size on setigers 7-14 or 15 (Figs 1C-D, 2A-B). Intersegmental ciliary bands on setigers 2-10 poorly-developed (Fig. 1A). Intrasegmental ciliary bands on setigers 2-4 poorly-developed, well-developed on setigers 5-16 (Fig. 1A). Interramal "genital" pouches absent. Pygidium unknown. Body color white in ethanol.

Notosetae capillary. Neurosetae include capillary setae, fringed setae, and bidentate hooded hooks. Capillary neurosetae of setigers 1-3 and 7-16 arranged in large superior bundle and small inferior bundle. Neuropodia of setigers 4-6 with two rows of 8-9 fringed setae each in superior bundle and 5-6 capillary setae in inferior bundle (Fig. 2C). Neuropodia from setiger 17 with 3-5 strongly-curved, bidentate hooded hooks alternating with paired capillary setae in the superior bundle; 2-6 capillary setae in the inferior bundle (Fig. 2D). Hooks with secondary tooth subdistal, inferior to large tooth; hood originating just below secondary tooth and terminating leaving tip of distal tooth exposed (Fig. 2E). Sabre setae absent.

**Etymology**. — This species is named for Dr. Kristian FAUCHALD in honor of his many contributions to polychaete systematics and for his support and friendship over the years.

**Distribution**. — Off Huntington Beach, southern California, 197 m.

**Remarks**. — *Pseudatherospio* closely resembles *Atherospio* Mackie & Duff, 1986 and *Pygospiopsis* Blake, 1983. Table 1 compares features in the three genera. The type material of *Atherospio disticha* Mackie & Duff, 1986 and *Pygospiopsis dubia* (Monro, 1930) was examined. All three genera possess a bilobed prostomium, a median occipital tentacle, notopodial lamellae fused to branchiae in setigers 7-12 up to 16, modified anterior neurosetae, and bidentate neuropodial hooks. The bidentate hooks have a small, secondary tooth inferior to the large tooth (Figs 2D,E). This arrangement of teeth is the reverse of what is usually found in the Spionidae, and readily unites these three genera as a group within the family. Contrary to the account of MACKIE & DUFF (1986), the hooks of *Pygospiopsis dubia* are mostly bidentate, with larger, more worn, hooks being unidentate or having a reduced inferior tooth.

TABLE 1. — Taxonomic characters of the genera *Pseudatherospio* gen. nov., *Atherospio* Mackie & Duff, 1986, and *Pygospiopsis* Blake, 1983.

| | *Pseudatherospio* | *Atherospio* | *Pygospiopsis* |
|---|---|---|---|
| Anterior prostomium | Bilobed | Bilobed | Bilobed |
| Occipital tentacle | Present | Present | Present |
| Branchiae | Setigers 1 to at least 36 | Setigers 7-12 | Setigers 2,3 and 7 to about 16 |
| Notopodial lamellae fused to branchiae | Setigers 7 to 15 or 16 | Setigers 7-12 | Setigers 7 to about 16 |
| Modified anterior neurosetae | Fringed, setigers 4-6 | Aristate, setigers 4-5 | Fringed, setigers 4-7 up to 9 |
| Posterior neuropodial hooded hooks | Bidentate | Bidentate | Uni-and bidentate |

Despite the similarity of branchial structure, the distribution of branchiae distinctly separates *Pseudatherospio*, *Pygospiopsis* and *Atherospio* from one another. Branchiae occur on setiger 1 to at least setiger 36 in *Pseudatherospio*, on setigers 2, 3 and 7 to about 16 in *Pygospiopsis* and on setigers 7 to 12 in *Atherospio*. The distribution of branchiae is an important generic level character in the Spionidae (see FAUCHALD, 1977 and FOSTER, 1971). For example, MACIOLEK (1990) separates *Spio* and *Microspio* based on the position of the first pair of branchiae (setiger 1 vs. setiger 2, respectively).

The presence of anterior neuropodial modified setae is not common in the Spionidae (see MACKIE & DUFF, 1986). *Pseudatherospio* and *Pygospiopsis* both have fringed neurosetae setae in setigers 4-6 and 4-7 up to 9, respectively. The presence of these fringed anterior neurosetae in *Pygospiopsis* was not reported in previous

Source : MNHN, Paris

accounts by MONRO (1930) or BLAKE (1983). *Atherospio* has aristate neurosetae in setigers 4-5. Two other spionid genera, *Scolecolepides* (Ehlers, 1907) and *Lindaspio* Blake & Maciolek, 1992, also have modified anterior neuropodial setae; but these genera can be separated based on the presence of prostomial frontal horns, the absence of an occipital tentacle, and the presence of notopodial modified hooks in posterior setigers (see MACIOLEK, 1984 and BLAKE & MACIOLEK, 1992).

The anteriorly bilobed prostomium, occipital tentacle, similarity of branchial structure, presence of modified anterior neurosetae, and structure of neuropodial hooded hooks all suggest that *Pseudatherospio*, *Atherospio*, and *Pygospiopsis* are a closely related, geographically wide-spread complex of genera. MACKIE (pers. comm.) is currently investigating the status of a second species of *Atherospio* from the south coast of England, as well as some related forms that appear to belong to two undescribed genera. One of the proposed new genera is present in the coastal waters of both the United Kingdom and Hong Kong, providing further evidence for a widely distributed complex.

## ACKNOWLEDGEMENTS

I would like to thank Dr. Doug DIENER MEC Analytical Systems and Tom GERLINGER, CSDOC, for making the material available. Thanks to Leslie HARRIS for her helpful discussion and examination of specimens; to Tom PARKER, County Sanitation Districts of Los Angeles County and Ron VELARDE, Metro Ocean Monitoring Program, City of San Diego for access to microscope facilities to produce drawings and photos. Funding for illustrations and reprints was made possible by Grants 92-2 and 94-1 from the Southern California Association of Marine Invertebrate Taxonomists. Illustrations were prepared by Julie SCHNEIDER. Special thanks to Dr. Kristian FAUCHALD, Andrew S.Y. MACKIE, Dr. Kirk FITZHUGH, Karen GREEN, Leslie HARRIS, Dr. James A. BLAKE, and an anomynous reviewer for their valuable comments. Thanks to Michelle PATZIUS for help in the production of the poster version presented at the Fourth International Polychaete Conference Angers, France. Finally, I would like to thank my wife, Jacqueline, and my children, Andrew and Robin, for their love and support during the preparation of this paper. This paper is Contribution No. 9 of the Southern California Association of Marine Invertebrate Taxonomists.

## REFERENCES

BLAKE, J.A., 1983. — Polychaetes of the family Spionidae from South America, Antarctica, and adjacent seas and islands. *Antarct. Res. Ser.* (American Geophysical Union), **39** : 205-288.

BLAKE, J.A. & N.J. MACIOLEK, 1992. — Polychaeta from deep-sea hydrothermal vents in the Eastern Pacific. III. A new genus and two new species of Spionidae from the Guaymas Basin and Juan de Fuca Ridge with comments on a related species from the Western Atlantic. *Proc. biol. Soc. Wash.*, **105** : 723-732.

FAUCHALD, K., 1977.— The polychaete worms. Definitions and keys to the orders, families, and genera. *Sci. Ser. Nat. Hist. Mus. Los Angeles County*, **28** : 1-190.

FOSTER, N.M., 1971. — Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. *Studies on the Fauna of Curacao and other Caribbean Islands*, **36** : 1-183.

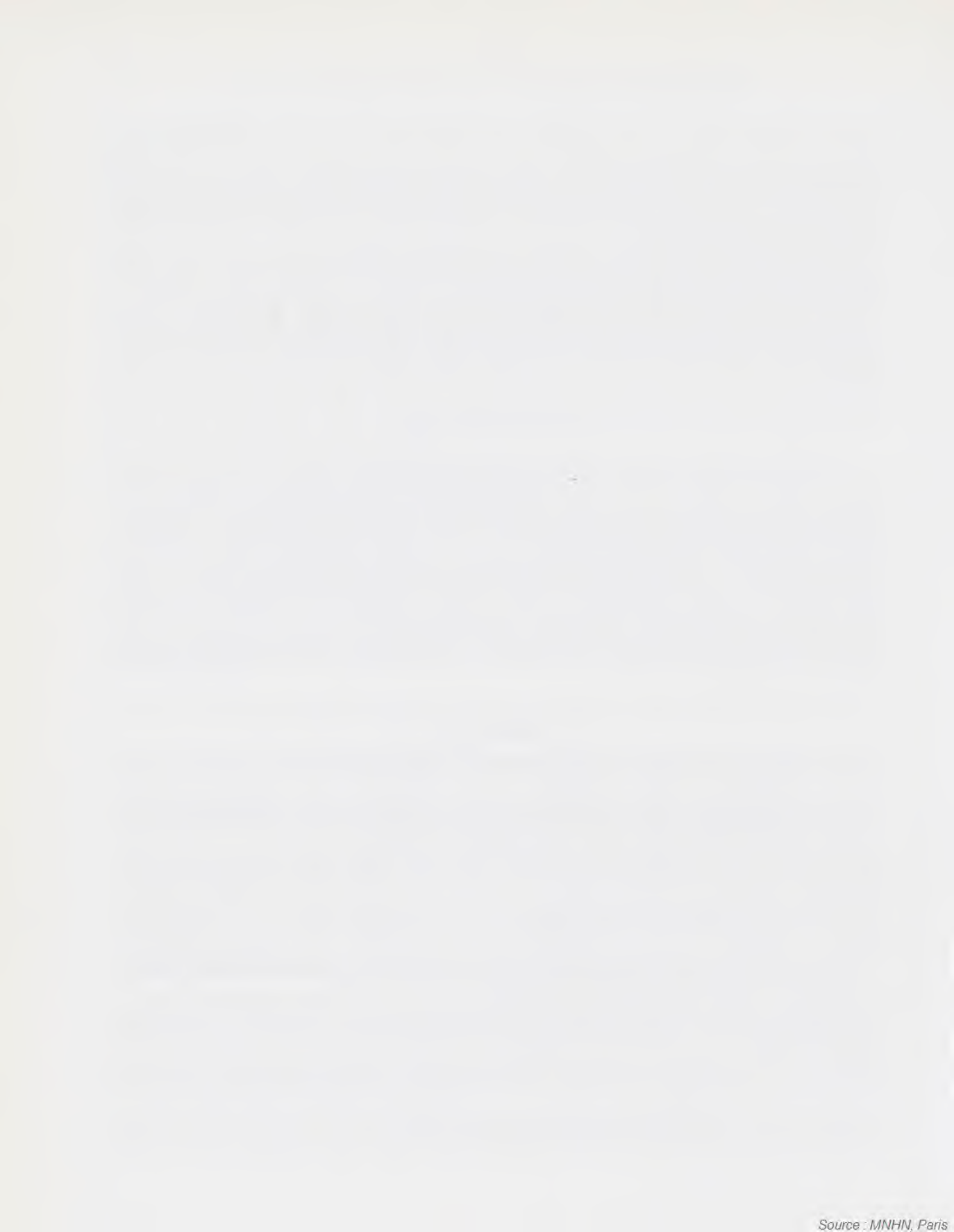
MACIOLEK, N.J., 1984. — New records and species of *Marenzelleria* Mesnil and *Scolecolepides* Ehlers (Polychaeta: Spionidae) from northeastern North America. *In*: P.A. HUTCHINGS (ed.), *Proc. First International Polychaete Conference*. Linnean Society of New South Wales : 48-62.

MACIOLEK, N.J., 1990. — A redescription of some species belonging to the genera *Spio* and *Microspio* (Polychaeta:Annelida) and descriptions of three new species from the northwestern Atlantic Ocean. *J. Nat. Hist.*, **24** : 1109-1141.

MACKIE, A.S.Y. & A.L. DUFF, 1986. — *Atherospio disticha* gen. et sp. nov. (Polychaeta:Spionidae) from Loch Tuirnaig, West Coast of Scotland. *Ophelia*, **25** : 139-146.

MONRO, C.A.A., 1930. — Polychaete Worms. *Discovery Rep.*, **2** : 1-222.

Source : MNHN, Paris



Source : MNHN, Paris

# *Adercodon pleijeli* gen. et sp. nov. (Polychaeta, Ampharetidae) from the Mediterranean Sea

*Andrew S. Y. MACKIE*

Department of Zoology
National Museum of Wales
Cathays Park
Cardiff CF1 3NP, Wales, UK

ABSTRACT

*Adercodon pleijeli* gen. et sp. nov. is described from muddy sediments (32-95 m depth) off Banyuls-sur-Mer, France and the east coast of Sicily, Italy. Characterised by 3 pairs of smooth branchiae, 13 thoracic setigers (paleae lacking), thoracic uncini from setiger 4 and papillose buccal tentacles the new form differs from all known ampharetid genera. Nevertheless, the possession of a ventral row of buccal teeth suggests an affinity with *Gnathampharete* Desbruyères, 1978. The arrangement and position of the teeth along the leading edge of the innermost ventral lip suggests that such teeth are functional and not an evolutionary remnant. Certain aspects of the taxonomy of the Ampharetidae are discussed.

RÉSUMÉ

***Adercodon pleijeli* gen. et sp. nov. (Polychètes Ampharetidae) en mer Méditerranée**

*Adercodon pleijeli* gen. et sp. nov. est décrit des substrats vaseux (32-95 m de profondeur) de Banyuls-sur-Mer, France et de Sicile orientale, Italie. Caractérisée par trois paires de branchies lisses, 13 sétigères thoraciques (pas de palées), des uncini thoraciques à partir du sétigère 4 et des tentacules buccaux pennés, la forme nouvelle se distingue de tous les autres genres d'Ampharétiens. Cependant, l'existence d'une série unique de dents buccales suggère une affinité avec *Gnathampharete* Desbruyères, 1978.

## INTRODUCTION

A small ampharetid worm that could not be assigned to any known genus was first noted during field collecting at Banyuls-sur-Mer, France in October 1991. The same animal was subsequently found in unidentified samples collected in Sicily the previous May. Later microscopical examination of specimens from both localities surprisingly revealed the presence of buccal teeth in addition to papillose tentacles. The new form is described and compared to *Gnathampharete paradoxa* Desbruyères, 1978, the only other ampharetid known to possess teeth.

---

MACKIE, A.S.Y., 1994. — *Adercodon pleijeli* gen. et sp. nov. (Polychaeta: Ampharetidae) from the Mediterranean Sea. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 243-250. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## MATERIALS AND METHODS

The specimens used in this study were obtained from dredge, or combined dredge and sledge, samples sieved using a 0.5 mm mesh. The latitude and longitudes of the Sicilian sampling positions were estimated from local landmarks, no position fixing system being available. Most specimens were sorted live and fixed in formalin (20-30 % in seawater), though some were obtained from bulk Mg $Cl_2$ relaxed samples prior to fixation in formalin (NMW.Z.1992.003.8-9) or Bouin's fluid (NMW.Z.1992.003.1-2). In all cases specimens were washed in freshwater prior to preservation in 80 % alcohol. All drawings were prepared with the aid of a camera lucida.

Epidermal glandular regions were highlighted by methyl green staining (NOLTE, 1913; HOFSOMMER, 1913; BANSE, 1970). Specimens were placed in a strong solution of stain, in 80 % alcohol, for about one minute. Excess stain was removed by a quick rinse using clean alcohol. The remaining staining pattern was then noted.

Type material was deposited in the following institutions: National Museum of Wales, Cardiff (NMW); Muséum National d'Histoire Naturelle, Paris (MNHN); Swedish Museum of Natural History, Stockholm (SMNH); United States National Museum of Natural History, Washington, D. C. (USNM); Australian Museum, Sydney (AM).

## SYSTEMATIC ACCOUNT

### *Adercodon* gen. nov.

TYPE SPECIES. — *Adercodon pleijeli* sp. nov.

DIAGNOSIS. — Prostomium trifid, lacking glandular ridges. Buccal cavity with papillose tentacles and single series of pointed teeth arranged along leading edge of innermost lower lip. Three pairs of smooth branchiae, arranged 2: 1 either side; posterior pair followed by pair of short nephridial papillae. Thirteen thoracic setigers from segment IV; paleae and modified notopodia lacking. Ten thoracic uncinigerous segments from setiger 4 (segment VII). Notosetae simple, capillary. Thoracic and abdominal uncini aviculopectinate. Pygidium with eyespots and circlet of anal cirri.

ETYMOLOGY. — The generic name is derived from *Aderkes* (Gr.) -unseen or unexpected, and *odous* (Gr.) -tooth. Gender, masculine.

### *Adercodon pleijeli* sp. nov.

Figs 1a-g; 2a-d

MATERIAL EXAMINED. — France. Banyuls-sur-Mer: sample 5, 42°30.17'N, 3°09.48'E, mud with detritus, 40 m, 7.X.91, two paratypes (NMW.Z.1992.003.6-7). — Sample 8, 42°29.75'N, 3°09.00'E, sandy mud, 32 m, 11.X.91, two paratypes (NMW.Z.1992.003.8-9). — Sample 11, 42°30.00'N, 3°16.50'E, muddy sand, 90 m, 14.X.91, one paratype (NMW.Z.1992.003.10), five paratypes (SMNH 4535). — Sample 12, 42°30.00'N, 3°11.75'E, mud, 80 m, 14.X.91, five paratypes (NMW.Z.1992.003.11-13), four paratypes (AM). — Sample 14, 42°29.90'N, 3°10.75'E, coarse sandy mud, 65 m, 15.X.91, one paratype (NMW.Z.1992.003.14). — Sample 15, 42°29.55'N, 3°09.90'E, mud with detritus, 45 m, 15.X.91, holotype (NMW.Z.1992.003.1), five paratypes (NMW.Z.1992.003.2-5), three paratypes (MNHN, UC 793), two paratypes (USNM 157618). — Italy. Sicily : sample T 8/9, off Aci Castello, 37°33.00'N, 15°10.70'E, muddy sand, 65-70 m, 16.V.90, four paratypes (NMW.Z.1992.002.1). — Sample T 15/17, off Aci Castello, 37°32.50'N, 15°10.80'E, muddy sand, 90-95 m, 17.V.90, two paratypes (NMW.Z.1992.002.2), 4 paratypes (SMNH 4536). — Sample T 32, off Castellucio (Brucoli), 37°17.00'N, 15°13.00'E, mud with detritus, 35-45 m, 22.V.90, two paratypes (NMW.Z.1992.002.3), four paratypes (MNHN, UC 794), four paratypes (USNM 157619). — Sample T 34/35, off Castellucio (Brucoli), 37°18.00'N, 15°13.00'E, mud with *Phyllochaetopterus*? tubes, 60-70 m, 23.V.90, one paratype (NMW.Z.1992.002.4).

DESCRIPTION. — Specimens small, 1.5-5.0 mm long (thoracic width 0.15-0.50 mm), with subcylindrical thorax and tapering abdomen. Holotype entire, 4.8 mm long (thoracic width 0.5 mm), with partially extruded upper (tentacular membrane) and lower lips (Fig. 1a) ; branchiae and almost all buccal tentacles missing.

Source : MNHN, Paris

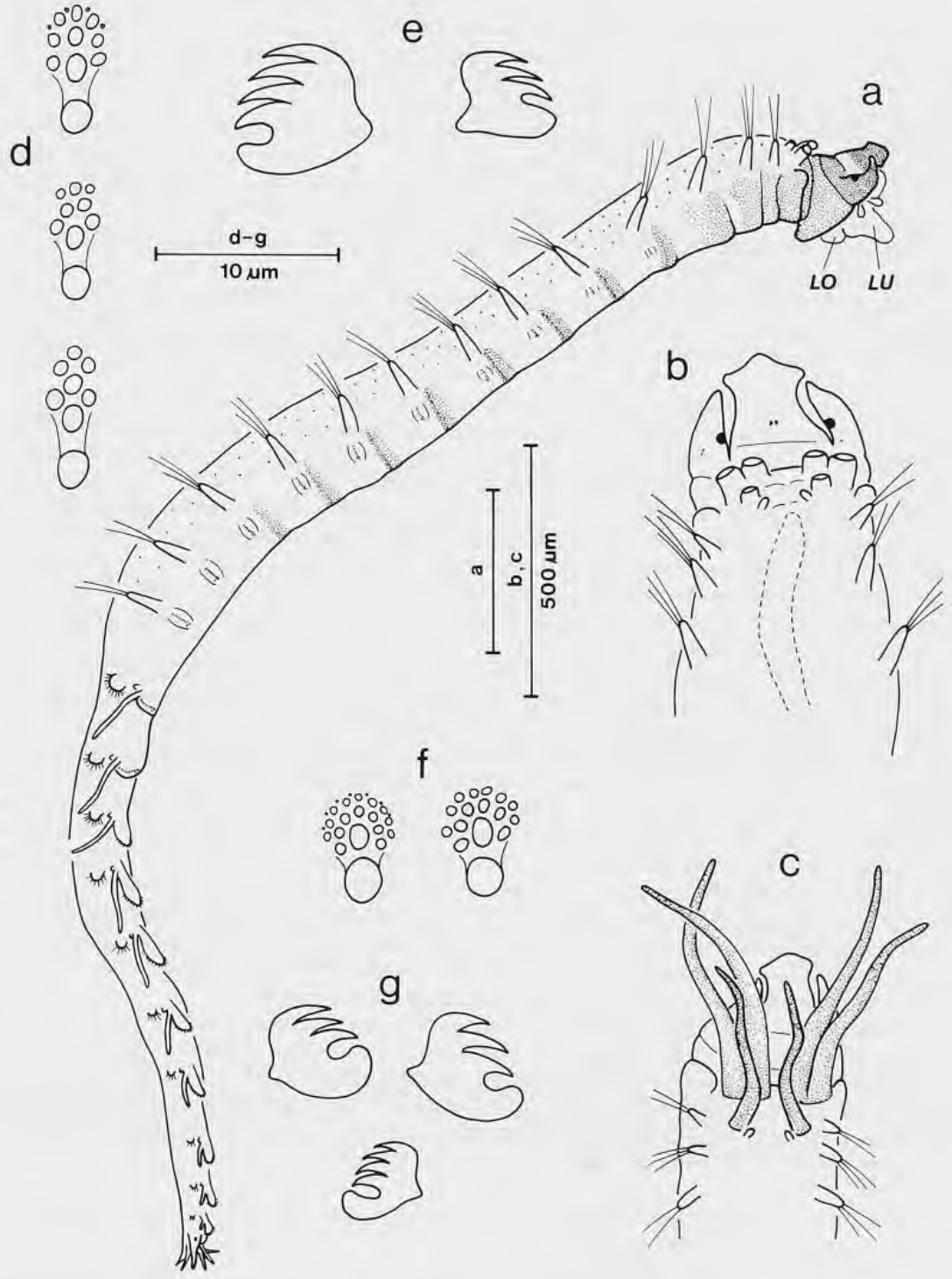



FIG. 1. — *Adercodon pleijeli*. (a, b: holotype; c: NMW.Z.1992.003.6; d-g: NMW.Z.1992.003.4-5): a, whole animal, lateral view (upper and outer lower lips partially extruded); shading represents methyl green staining. — b, head region, dorsal view (branchiae lacking). — c, head region, dorsal view. — d, thoracic uncini, frontal view. — e, thoracic uncini, lateral view.— f, abdominal uncini, frontal view. — g, abdominal uncini, lateral view. Abbreviations: *LO*, outermost lower lip; *LU*, upper lip.

Source : MNHN, Paris

Prostomium trifid (Fig. 1b); median part bell-shaped, anterior margin broadly rounded to triangular; lateral lobes curved, pointed, only basally united to median part. Single pair of round red-brown eyes posterolaterally, near points of fusion of prostomial lobes; several small black supplementary eyespots medially and laterally at approximately same level. Segment I visible as complete ring, ventral part forming lower margin of mouth. Segment II narrower than segment I, largely hidden by segment III.

Buccal tentacles retractile, papillose; each densely ciliated with bilaterally arranged papillae (Fig. 2b). Tentacular papillae long, filiform; each with swollen tip bearing distal tuft of cilia. Buccal cavity ventrally with single curved and unbroken row of 30-40 triangular teeth along leading edge of innermost lip (Figs 2a, c). In profile, teeth appear V-shaped. From examination of slide preparations each tooth revealed to be sub-conical, laterally compressed and hollow (Fig. 2d); superior root somewhat flared terminating in large projecting peg; inferior root long, slender and tapered.

Three pairs of ciliated cirriform branchiae (Fig. 1c); anterior 2 pairs basally fused, separated by medial gap, arranged transversely at level of segment III; third pair, shorter, more slender, arising separately behind anterior pairs. Third branchial pair followed by pair of short rounded nephridial papillae in slightly more medial position (Figs 1b, c).

Segment III collar-like, slightly expanded dorsolaterally forming rounded lobes; paleae lacking. Thirteen thoracic setigers from segment IV; notopodial lobes cylindrical, well-developed with 4-8 slender sheathed capillary setae; modified notopodia and notosetae lacking. Ten thoracic uncinigerous segments from setiger 4 ; anterior neuropodial tori inconspicuous with 2-5 uncini, posterior neuropodia more noticeable with 9-12 uncini in vertical row (usually one lower uncinus situated posterior to row on all except first few anterior uncinigers). Uncini small with main fang surmounted vertically by one supplementary tooth (latter sometimes lacking), both together being surrounded cowl-like by one or two rows of 5-8 secondary teeth (Fig. 1d) ; second row of small denticles often inconspicuous. Some larger uncini with two supplementary teeth vertically above main fang; others slightly asymmetrical with secondary teeth arranged in two uneven vertical rows. In profile uncini aviculopectinate with apparent vertical series of 3-5 teeth (Fig. 1e).

Ten abdominal setigers; neuropodial tori of anterior two setigers similar to those of thorax (including arrangement of uncini), remaining neuropodia developed as extended pinnules. Each neuropodial pinnule with 6-14 uncini individually situated on distal tips of single series of digitiform projections along outer margin; uncini attached by long tendons. Uncini initially similar to those of thorax but by third or fourth abdominal setiger most lack supplementary teeth in vertical position above main fang and uncini become smaller, more squat and rounded in appearance. These and all other abdominal uncini with main fang surrounded by two obvious rows of 6-9 secondary teeth (Fig. 1f); third row of tiny denticles sometimes visible. In profile uncini aviculopectinate with apparent vertical series of 3 or 4 teeth (Fig. 1g). Each neuropodium with single cirrus arising from superior margin; cirri long and very conspicuous on anterior 5 or 6 setigers, becoming increasingly shorter towards pygidium (Fig. 1a). Abdominal notosetae lacking but single small rounded ciliated tubercles evident in notopodial positions (inconspicuous on posteriormost segments). Small triangular papilla evident between each neuropodial cirrus and ciliated tubercle. Pygidium with terminal anus surrounded by circlet of about six cirriform papillae. Lateral pair of anal cirri more robust, basally with single small black eyespots.

Use of methyl green (Fig. 1a) revealed intense staining of pre-branchial region, particularly on prostomial lobes. Staining of segments I and II slightly lighter. Lateral and ventral parts of segments III-V (setiger 2) similarly stained. Thereafter (until setiger 11) staining largely restricted to presetal lateral/ventral bands. Dorsal region of thorax largely unstained; staining only evident as small widely scattered spots. Abdomen unstained.

Specimens (in alcohol) yellowish or pinkish white. Some specimens with remnants of thin mucous tube. Many specimens ovigerous; ova large, rounded, up to 125 µm diameter.

ETYMOLOGY. — It is a pleasure to name this new species after Dr. Fredrik PLEIJEL, my good friend and fellow researcher, in recognition of his work on the Polychaeta.

HABITAT. — The new species occurs in muddy sediments, with or without terrestrial/seagrass detritus, in shallow shelf depths (< 100 m). The physical and biological characteristics of the type locality off Banyuls have been detailed previously by GOT *et al.* (1968), GUILLE & SOYER (1968, 1970) and GUILLE (1970). The species was found throughout the four subdivisions of the *Amphiura filiformis* community as recognised by GUILLE & SOYER (1970): *Scoloplos armiger* faciès (samples 8 & 15), *Venus ovata* subcommunity (samples 5 & 14), *Nucula sulcata* subcommunity (sample 12) and *Auchenoplax crinata* subcommunity (sample 11). However, in all cases its occurrence was low (one to six per dredge sample).

Source : MNHN, Paris

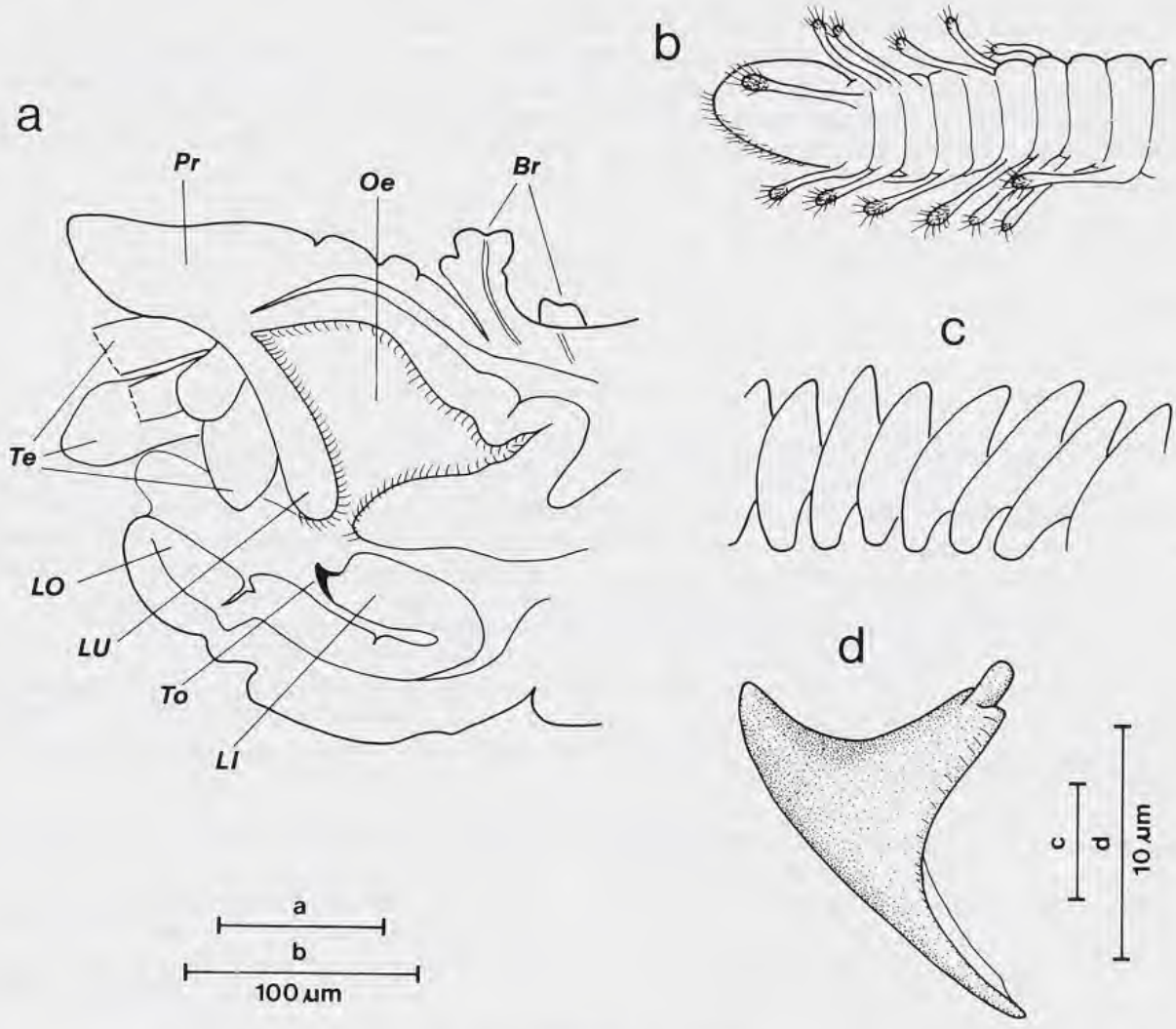



FIG. 2. — *Adercodon pleijeli*. (a: NMW.Z.1992.003.8; b: NMW.Z.1992.003.10; c: NMW.Z.1992.003.7): a, head region, sagittal section. — b, distal region of tentacle, dorsal view. — c, portion of row of buccal teeth, ventral view. — d, derived shape of individual buccal tooth, lateral view. Abbreviations: *Br*, branchia; *LI*, innermost lower lip; *LO*, outermost lower lip; *LU*, upper lip; *Oe*, oesophagus; *Pr*, prostomium; *Te*, tentacle; *To*, tooth.

Information on the benthos off eastern Sicily is more limited (see GAMBI *et al.*, 1985, for bibliography). CANTONE (1970) and CANTONE & FASSARI (1983) provide some information on the polychaetes present in the Gulf of Catania region where *Adercodon* was found.

REMARKS. — According to the literature (e.g. FAUCHALD, 1977; HOLTHE, 1986c), *Muggoides cinctus* Hartman, 1965 is the only other member of the Ampharetinae to possess three pairs of branchiae and 13 thoracic setigers with the last 10 uncinigerous. *Adercodon pleijeli* differs markedly in having buccal teeth and papillose (not smooth) tentacles, and in lacking dorsally displaced notopodia and modified notosetae. The presence of buccal

Source : MNHN, Paris

teeth appears to ally *Adercodon* with *Gnathampharete* Desbruyères, 1978, the only other ampharetid known to have similar structures. *Adercodon* differs notably in having only three pairs of smooth branchiae rather than four pairs of pennate ones, in having 13 thoracic setigers with 10 uncinigerous rather than 14 with 12, and in lacking paleae.

Consideration of certain selected characters could possibly align the genus with other genera however, in each case, the differences between the taxa seem more numerous than the similarities. For example, while *Decemunciger* Zottoli, 1982 has the same thoracic complement, it differs in having four pairs of branchiae and smooth tentacles, and in lacking anal cirri. *Ymerana* HOLTHE, 1986 would likewise have the same thoracic complement should the expanded and asetous notopodial expansions of the setiger 14 be interpreted as abdominal rather than thoracic. Even so, this genus differs in having smooth tentacles; the form of the branchiae and pygidial region are unknown.

It should be noted that *Gnathampharete* was reported as lacking buccal tentacles and HOLTHE (1986c: 46) considered this to be the normal condition in this genus. However, HOLTHE (pers. commn.) informs me that he has recently re-examined the holotype of *G. paradoxa* and found some deeply retracted tentacles. He was unable to determine whether these were papillose or smooth.

## DISCUSSION

It may be significant that the majority of recently described genera (e.g. *Gnathampharete* Desbruyères, 1978 ; *Decemunciger* Zottoli, 1982; *Endecamera* Zottoli, 1982; *Zatsepinia* Jirkov, 1986; *Ymerana* Holthe, 1986) are small, generally less than 10 mm long. An increased use of sieves with meshes of 0.5 mm or less, coupled with an increase in deeper water investigations, makes it inevitable that many more species await discovery. A number of these may well be referrable to genera that are currently monotypic. Alternatively they may provide additional taxonomic information that will facilitate the synonymy of some such genera. For the present, I believe it better to erect new genera than to confuse things further by prematurely expanding existing generic diagnoses.

All the characters separating *Adercodon* gen. nov. from other ampharetids have been, and still are, used to define ampharetid genera (DAY, 1964 ; FAUCHALD, 1977; HOLTHE, 1986a, c). The resulting profusion of monotypic genera has increasingly led to questions (e.g. DAY, 1964; CHARDY & DESBRUYÈRES, 1979; HOLTHE, 1986b, c) concerning the relative "usefulness" of the characters and the apparent narrowness of many generic diagnoses. As yet there have been no new approaches to the problem.

One thing that has received little attention (but see HOLTHE, 1986c: 19-20) is the possible generic consequences of re-assigning certain anterior abdominal setigers to the thorax. GEORGE (1979) noted that *Sabellides octocirrata* (Sars, 1835) had the same type of uncini on 13 anterior segments, the last two lacking notopodia, and considered these all thoracic. *Sabellides* is, however, more usually cited (DAY, 1964; FAUCHALD, 1977; HOLTHE 1986a, c) as having 11 thoracic uncinigerous segments. In *Adercodon,* the abdominal uncini of the anterior two abdominal setigers are borne on "sessile" tori identical to those of the thorax whereas the remainder differ, being situated on long projecting pinnules. On this basis *Adercodon* could be said to have 15 thoracic setigers, the last 12 being uncinigerous. Such observations suggest that a re-examination of the 'thoracic' complements in all ampharetids could perhaps be a fruitful line of investigation.

The enigmatic presence of buccal teeth in *Gnathampharete* and the possible phylogenetic implications concerning the Ampharetidae and Terebellida as a whole were discussed by DESBRUYÈRES (1978) and HOLTHE (1986c). Both workers considered these to be possible representations of an ancestral condition and the latter postulated that they were probably not functional. The discovery of well-defined teeth in *Adercodon* in addition to papillose tentacles may indicate otherwise. Their position, form and arrangement along the edge of the innermost ventral lip strongly suggests that they are indeed functional. They could be involved in sorting the particles collected by the tentacles; deposit-feeding on the sediment surface being the most common feeding method in the Ampharetidae (FAUCHALD & JUMARS, 1979). On the other hand (though perhaps less likely), it may be that certain ampharetids are, in some way, predatory. Ingestion of larval invertebrates has been noted in a number of ampharetids and other members of the Terebellida (FAUCHALD & JUMARS, 1979; WILSON, 1980; ZOTTOLI, 1982), though it is unclear whether this was an active or passive process.

Although earlier detailed morphological studies on the Ampharetidae (FAUVEL, 1897; HESSLE, 1917) made no mention of buccal teeth, I agree with HOLTHE (1986c) in believing that they may be more common than thought. Further investigation, particularly of the smaller species, could prove rewarding. Certainly the more characters that can be detailed for the Ampharetidae, the more chance we have of re-evaluating the status of the genera and their phylogenetic relationships.

Source : MNHN, Paris

## ACKNOWLEDGEMENTS

I would like to thank Alain GUILLE and his staff for access to laboratory and sampling facilities at the Laboratoire Arago in 1991 and Philippe BOUCHET for inviting me to join the Fifth European Marine Malacological Workshop in Sicily the previous year. For both field trips I am indebted to all who helped with the collecting; especially Philippe BOUCHET, Rudo von COSEL and Anders WARÉN in Sicily, and the crews of the R.V. *Nereis* and dive boat *Rufi* in Banyuls. I gratefully acknowledge the National Museum of Wales for funding both visits. Special thanks to Fredrik PLEIJEL, my co-worker on both sampling trips, for all his help, advice and discussions. Fredrik Pleijel and Annette Woodham kindly commented on an early draft of this paper. Thanks also to Torleif HOLTHE who, as one of the referees, allowed me to refer to his unpublished observations.

## REFERENCES

BANSE, K., 1970. — The small species of *Euchone* Malmgren (Sabellidae, Polychaeta). *Proc. biol. Soc. Wash.*, **83** : 387-408.

CANTONE, G., 1971. — Ricerche sui Policheti della Sicilia. I. *Boll. Sed. Accad. gioenia Sci. nat.*, (4) **10** : 914-944.

CANTONE, G. & FASSARI, G., 1983. — Polychaetous annelids of soft bottoms around the Gulf of Catania (Sicily). *Rapp. P. -v. Réun. Commn int. Explor. scient. Mer Méditerr.*, **28** : 251-252.

CHARDY, P. & DESBRUYÈRES, D., 1978. — La classification multicritère. Application à la révision de la sous-famille des Ampharetinae (Annélides polychètes). *Année biol.*, **18** : 521-537.

DAY, J. H., 1964. — A review of the family Ampharetidae (Polychaeta). *Ann. S. Afr. Mus.*, **48** : 97-120.

DESBRUYÈRES, D., 1978. — Un Ampharetidae (Annélides polychètes sédentaires) à structure buccale aberrante: *Gnathampharete paradoxa* gen. sp. n. *C. r. hebd. Séanc. Acad. Sci., Paris*, (D) **286** : 281-284.

FAUCHALD, K., 1977. — The polychaete worms. Definitions and keys to the orders, families and genera. *Sci. Ser. nat. Hist. Mus. Los Ang. Cty*, **28** : 1-188.

FAUCHALD, K. & JUMARS, P. A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanography mar. Biol.*, **17** : 193-284.

FAUVEL, P., 1897. — Recherches sur les Ampharétiens, annélides polychètes sédentaires, morphologie, anatomie, histologie, physiologie. *Bull. scient. Fr. Belg.*, **30** : 277-488.

GAMBI, M. C., BIANCHI, C. N., GIANGRANDE, A. & COLOGNOLA, R., 1985. — Per un censimento della polichetofauna delle coste Italiane, nota preliminare. *Oebalia*, **11** : 289-302.

GEORGE, J. D., 1979. — The polychaetes of Lewis and Harris with notes on other marine invertebrates. *Proc. R. Soc. Edinb.*, **77B** : 189-216.

GOT, H., GUILLE, A., MONACO, A. & SOYER, J., 1968. — Carte sédimentologique du plateau continental au large de la côte catalane française (P. O.). *Vie Milieu*, (B) **19** : 273-290.

GUILLE, A., 1970. — Bionomie benthique du plateau continental de la côte catalane française. II- Les communautés de la macrofaune. *Vie Milieu*, (B) **21** : 149-280.

GUILLE, A. & SOYER, J., 1968.— La faune benthique des substrats meubles de Banyuls-Sur-Mer. Premières données qualitatives et quantitatives. *Vie Milieu*, (B) **19** : 323-359.

GUILLE, A. & SOYER, J., 1970. — Bionomie benthique du plateau continental de la côte catalane française. I- Physiographie. *Vie Milieu*, (B) **21** : 137-147.

HARTMAN, O., 1965. — Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occ. Pap. Allan Hancock Fdn*, **28** : 1-377.

HESSLE, C., 1917. — Zur Kenntnis der terebellomorphen Polychæten. *Zool. Bidr. Upps.*, **5** : 39-258.

HOFSOMMER, A., 1913. — Die Sabelliden-Ausbeute der "Poseidon"-Fahrten und die Sabelliden der Kieler Bucht. *Wiss. Meeresunters. (Kiel.)*, **15** : 305-364.

HOLTHE, T., 1986a. — Polychaeta Terebellomorpha. *Mar. Invert. Scandinavia*, **7** : 1-194.

Source : MNHN, Paris

HOLTHE, T., 1986b. — Polychaeta Terebellomorpha from the northern Norwegian Sea and the Polar Sea, with descriptions of *Mugga bathyalis* sp. n. and *Ymerana pteropoda* gen. and sp. n. *Sarsia*, **71** : 227-234.

HOLTHE, T., 1986c. — Evolution, systematics, and distribution of the Polychaeta Terebellomorpha, with a catalogue of the taxa and a bibliography. *Gunneria*, **55** : 1-236.

JIRKOV, I. A., 1986. — *Zatsepinia rittichae* gen. et sp. n. (Polychaeta, Ampharetidae) from the Norwegian and Barents Sea. *Zool. Zh.*, **65** : 289-290.

NOLTE, W., 1913. — Zur Kenntnis der Maldaniden der Nord- und Ostsee. *Wiss. Meeresunters. (Kiel.)*, **15** : 1-94.

WILSON, W. H. 1980. — A laboratory investigation of the effect of a terebellid polychaete on the survivorship of nereid polychaete larvae. *J. exp. mar. Biol. Ecol.*, **46** : 73-80.

ZOTTOLI, R., 1982. — Two new genera of deep-sea polychaete worms of the family Ampharetidae and the role of one species in deep-sea ecosystems. *Proc. biol. Soc. Wash.*, **95** : 48-57.

Source : MNHN, Paris

# The genus *Ophryotrocha* sensu lato (Polychaeta, Dorvilleidae) in the Tromsø area, northern Norway

*Eivind OUG*

Norwegian Institute for Water Research
Regional Office Sørlandet
Televeien 1
N-4890 Grimstad, Norway

ABSTRACT

Five species of small dorvilleids, here referred to the genus *Ophryotrocha* Claparède & Mecznikow, 1869, have been collected from shallow-water soft-bottom areas near Tromsø, Norway. The species are *O. baccii* Parenti, 1961, *O.* cf. *scarlatoi* Averincev, 1989, *O. cosmetandra* Oug, 1990, *O.* cf. *puerilis*, and one species which is probably new to science. In *O.* cf. *scarlatoi* the last 7-9 segments and pygidium are rimmed by a pair of scalloped longitudinal folds arising dorsolaterally and appearing to curve and meet across the dorsum. The presumed new species is close to *O. littoralis* (Levinsen, 1879) in having similar mandibles with four strong teeth. It differs from this species in having a smaller size, in the shape of the palps, and in details of the maxillae. The genus *Mammiphitime* Orensanz, 1990, erected for forms similar to *O. cosmetandra*, is discussed.

RÉSUMÉ

**Le genre *Ophryotrocha sensu lato* (Polychaeta, Dorvilleidae) dans la région de Tromsø, nord de la Norvège.**

Cinq petites espèces de Dorvilleidiens du genre *Ophryotrocha* Claparède & Mecznikow, 1869, ont eté récoltées dans les sédiments meubles peu profonds da la région de Tromsø, au nord de la Norvège. Les espèces sont *O. baccii* Parenti, 1961, *O.* cf. *scarlatoi* Averincev, 1989, *O. cosmetandra* Oug, 1990, *O.* cf. *puerilis*, et une espèce qui probablement est nouvelle pour la science. Chez *O.* cf. *scarlatoi* les derniers 7-9 segments et le pygidium portent dorsalement des plis longitudinaux. Ces plis ont un bord formé comme des vagues, ils se courbent et se rencontrent dans la face dorsale. L'espèce supposée nouvelle est proche de *O. littoralis* (Levinsen, 1879) parce qu'elle a des mâchoires inférieures avec quatre fortes dents. L'espèce se distingue de *O. littoralis* par sa petite taille, par la forme de ses palpes et par ses mâchoires supérieures. Le genre *Mammiphitime* Orensanz, 1990, établi pour quelques espèces ressemblant à *O. cosmetandra*, est décrit et commenté.

---

OUG, E., 1994. — The genus *Ophryotrocha sensu lato* (Polychaeta, Dorvilleidae) in the Tromsø Area. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 251-257. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

During benthic surveys in the vicinity of Tromsø, Norway, five species referred to the dorvilleid genus *Ophryotrocha* Claparède & Mecznikow, 1869 have been found. The samples were taken in 1980-91, but most specimens were collected during an environmental impact assessment survey in 1983 (OUG *et al.*, 1985). The specimens have been found in shallow water or at moderate depths (< 25 m).

One of the species is probably new to science, but it is close to *Ophryotrocha littoralis* (Levinsen, 1879) from Greenland. Type specimens of this species were examined for comparison, especially with regard to maxillary parts.

The genus *Ophryotrocha* contains about 30 species. A number of species are similar, but some recently described species show unusual features not seen in typical forms of the genus. In a recent revision of *Ophryotrocha* HILBIG & BLAKE (1991) discussed the character variations, but found it impossible to split the genus into less heterogeneous new genera. However, ORENSANZ (1990) erected the new genera *Mammiphitime*, *Pinniphitime* and *Palpiphitime* for species with special morphological traits. ORENSANZ (1990) further argued in favour of separating *Ophryotrocha* and allied forms from the other dorvilleids. He proposed to transfer the "ophryotrochas" to the family Iphitimidae, consequently revising the definitions of Dorvilleidae and Iphitimidae. The species collected in the Tromsø area are presently assigned to *Ophryotrocha* (in the wider sense), but the need for a revision of the genera is acknowledged.

## METHODS

Tromsø is located in a fjord area sheltered from the open sea (Fig. 1). Annual sea temperature and salinity variations are 2-10 °C and 31-33 P.S.U. respectively, but higher temperatures and lower salinities may occur in surface waters.

Samples were taken using a 0.1 $m^2$ van Veen grab or a modified light-weight Ockelmann detritus sled. The collected material was sieved through a 1 mm screen and preserved in 4 % formaldehyde solution. The material was subsequently transferred to 70 % alcohol.

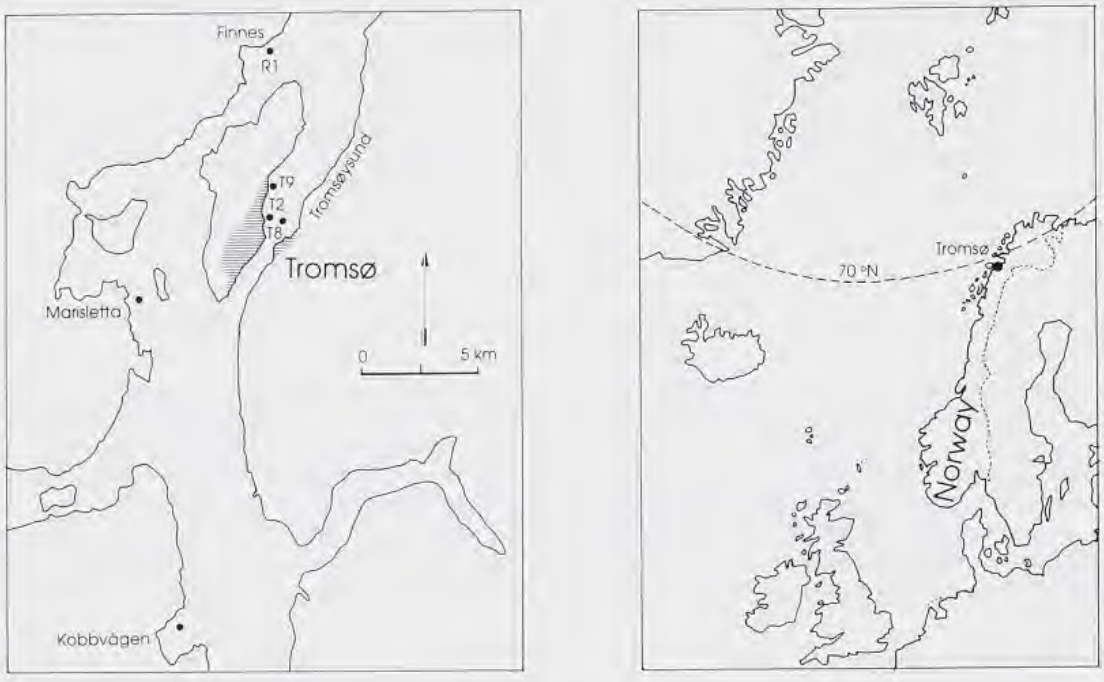



FIG. 1. — Map showing location of Tromsø, northern Norway (left) and sampling stations (right). Station numbers refer to the environmental impact assessment study in 1983 (OUG *et al.*, 1985).

Source : MNHN, Paris

Specimens in alcohol or glycerine were examined for general morphology. Parapodia were removed and mounted in glycerol for examination of setae and parapodial structures. Pharyngeal structures were removed by dissection and mounted in glycerine or (permanent mounts) in Eukitt or Gurr's Hydramount direct mounting medium. Drawings were made primarily with the aid of a Leitz camera lucida attachment.

## SYSTEMATICS

### *Ophryotrocha baccii* Parenti, 1961

Fig. 2 a-g

*Ophryotrocha baccii* Parenti, 1961: 438-440, fig. I: 1-5, fig. II: 6-7. — HILBIG & BLAKE, 1991
*Ophryotrocha bacci*. — ÅKESSON, 1973. — GEORGE & HARTMANN-SCHRÖDER, 1985

MATERIAL EXAMINED. — Kobbvågen, 27 Nov. 1980, 6 m, mud with $H_2S$: six specimens. — Tromsøysund, 24 March 1983, 7m (stn T9), sand-mixed mud: 20 specimens.

DESCRIPTION. — Complete specimens 4.0-4.5 mm long, 0.5-0.8 mm wide excluding parapodia, with 30-38 setigers. Prostomium with digitiform antennae and similar ventrolateral palps (Fig. 2a). Parapodia with distinct acicular lobes and digitiform dorsal and ventral cirri (Fig. 2d). Setae of three kinds: dorsal to acicula 3-5 capillary setae, distally slightly dilated, with an apical curved tooth (Fig. 2e), ventral to acicula 4-7 compound setae (Fig. 2f) and one needle-thin unjointed inferior seta emerging from setal lobe (Fig. 2g). Mandibles strongly chitinized, each piece with two distinct serrated teeth (Fig. 2b). Maxillae of p-type, with forceps and seven pairs of denticles in two rows (Fig. 2c).

REMARKS. — The specimens fit the original description of *O. baccii* well, except that the maximum number of segments (38) is greater, and most specimens have a few more bristles than stated by PARENTI (1961). The mandibles differ slightly in shape by having distinct flat, less chitinized lateral projections behind the teeth (Fig. 2b). Sectioned specimens examined for gonadal products had sperm in 2-3 anterior segments and eggs in the next approximately 20 segments. ÅKESSON (1973) classified *Ophryotrocha baccii* as a contemporary hermaphrodite with anterior male and posterior female trunk regions.

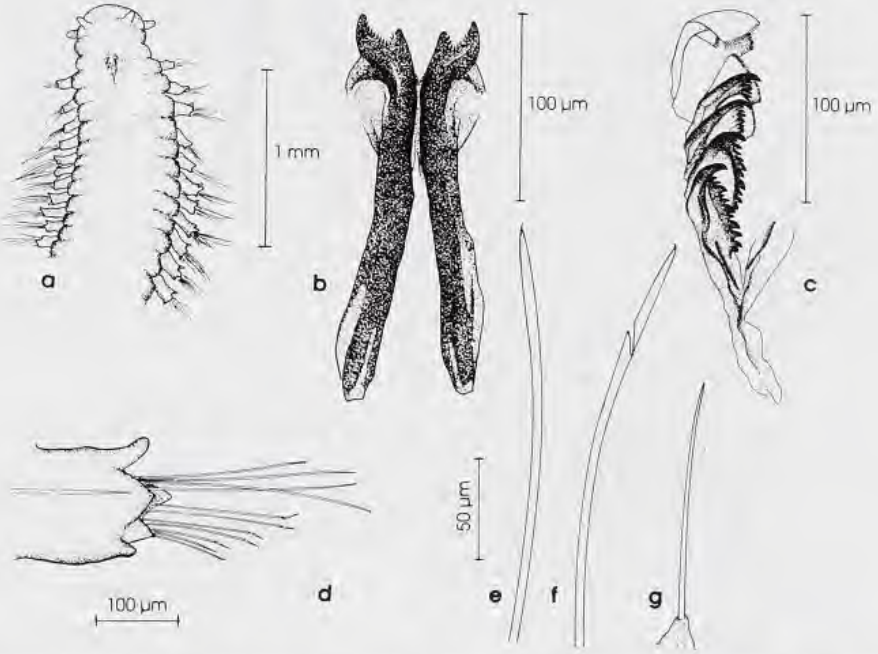



FIG. 2. — *Ophryotrocha baccii*: **a**, anterior end, dorsal view. **b**, mandibles. **c**, maxillae, forceps and left denticle row. **d**, parapodium, setiger 16. **e**, supra-acicular simple seta. **f**, subacicular compound seta. **g**, inferior simple seta.

Source : MNHN, Paris

DISTRIBUTION. — The species is previously known from France (Roscoff), The British Isles and the Swedish west coast (ÅKESSON, 1973 ; GEORGE & HARTMANN-SCHRÖDER, 1985).

## *Ophryotrocha cf. scarlatoi* Averincev, 1989

Fig. 3 a-h

MATERIAL EXAMINED. — Marisletta, 27 Nov. 1980, 15 m, dark mud with $H_2S$: four specimens, — Tromsøysund, 24 March 1983, 7 m (stn T2), black mud with $H_2S$: one specimen, 24 March 1988: 1 specimen, — Finnes, 24 March 1983, 7 m (stn R1), sand-mixed mud: one specimen.

DESCRIPTION. — Complete specimens 4.5-6 mm long, 0.5-0.6 mm wide excluding parapodia, with 26-34 setigers. Last 7-9 segments and pygidium rimmed by two scalloped longitudinal folds arising dorsolaterally and curving across the dorsum (Fig. 3a). Setae of four kinds: dorsal to acicula 2-3 thin gradually tapering capillary setae (Fig. 3e) and 2-4 shorter blunt capillary setae (Fig. 3f), ventral to acicula 5-10 compound setae with blunt-tipped blades (Fig. 3g) and one, occasionally two, unjointed inferior seta emerging from the tip of the setal lobe (Fig. 3h). Some setae with very fine subdistal serration. Maxillae of p-type, with enlarged forceps and seven pairs of denticles in two rows (Fig. 3c). Some specimens with eggs from setiger 7 to about setiger 20.

REMARKS. — The description of *Ophryotrocha scarlatoi* by AVERINCEV (1989) is brief and illustrated with simple drawings. Details of jaw elements are not given. The specimens from Tromsø seem to differ by having slimmer mandibles and bristles with weak or no serrations. A similar form from the Canadian Arctic (FOURNIER & CONLAN, 1994), which may belong to *O. scarlatoi*, seems to differ from the Tromsø specimens in having somewhat shorter mandibles, in details of maxillary parts, and in having a ventral cirrus on posterior parapodia.

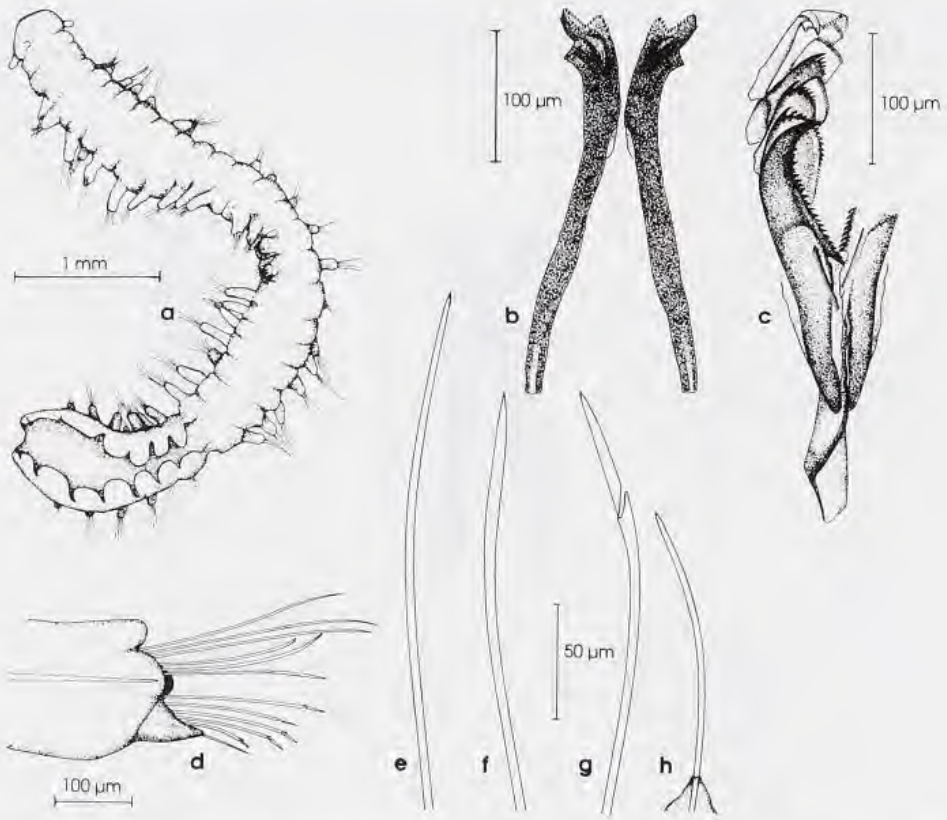



FIG. 3. — *Ophryotrocha* cf. *scarlatoi*: **a**, complete specimen, dorsal view. **b**, mandibles. **c**, maxillae, forceps and left denticle row. **d**, parapodium, setiger 13. **e**, **f** supra-acicular simple setae. **g**, subacicular compound seta. **h**, inferior simple seta.

Source : MNHN, Paris

DISTRIBUTION. — *Ophryotrocha scarlatoi* is previously reported only from Franz Joseph Land (AVERINCEV, 1989). The species may have a wide distribution in the Arctic.

### ***Ophryotrocha cosmetandra*** Oug, 1990

REMARKS. — This species shows a strong sexual dimorphism. Mature males are characterized by conspicuous dorsolateral processes on the posterior segments and the pygidium. Only males show the K-type maxillae. Both sexes are further distinguished by setal morphology and mandibles with three strong teeth (OUG, 1990).

ORENSANZ (1990) erected the genus *Mammiphitime*, belonging to the revised family Iphitimidae, for some *Ophryotrocha*-related forms with conspicuous dorsal lobes. The species *Mammiphitime tridentata* Orensanz, 1990 from the southern Atlantic is similar to *O. cosmetandra* in a number of characters, e.g. the shape of the mandibles with three strong teeth and compound setae of the spiniger type only. Sexual dimorphism was not described. It seems that *O. cosmetandra* and *M. tridentata* should be referred to the same genus, but *Mammiphitime*, if adopted, may need to be redefined.

DISTRIBUTION. — *O. cosmetandra* is the most common dorvilleid in the Tromsø area. It is known from northern Norway and Greenland (see OUG, 1990 for records) and has recently also been collected in organically polluted harbours in the Faroes (M.E. Petersen, pers. comm).

### ***Ophryotrocha*** cf. ***puerilis*** Claparède & Mecznikow, 1869

*Ophryotrocha puerilis*. — FAUVEL, 1923. — LA GRECA & BACCI, 1962

MATERIAL EXAMINED. — Tromsøysund, 24 March 1983, 25 m (stn T8), sandy mud with gravel and shell fragments: one specimen.

REMARKS. — The specimen fits the descriptions of *Ophryotrocha puerilis* given by PARENTI (1961), LA GRECA & BACCI (1962) and HARTMANN-SCHRÖDER (1971), except for the mandibles which appear to have more than two teeth. The mandibles, however, are worn and presumably damaged. The specimen has K-type maxillae. Eggs are visible in setigers 8 to 16.

*Ophryotrocha puerilis* has repeatedly been confused with other species (ÅKESSON, 1973, 1984). Present descriptions, mostly showing outline drawings of jaw parts, are presumably insufficient or inacurrate for critical species discrimination. Reports of *O. puerilis* from world-wide areas may represent a confusion of related species.

DISTRIBUTION. — The confirmed distribution is in the Mediterranean Sea (ssp. *O. p. puerilis*) and the eastern North Atlantic (ssp. *O. p. siberti*) (ÅKESSON, 1973, 1984 ; GEORGE & HARTMANN-SCHRÖDER, 1985).

### ***Ophryotrocha*** sp.
Fig. 4 a-h

MATERIAL EXAMINED. — Marisletta, 27 Nov. 1980, 6-10 m, soft sand-mixed mud: one specimen, 15 June 1987: two specimens.

DESCRIPTION. — Largest specimen 3.4 mm long for 28 setigers, width 0.3 mm excluding parapodia (Fig. 4a). Prostomium with two dorsal digitiform antennae and two ventrolateral small sphaerical to ovoid faintly visible palps. Parapodia uniramous (Fig. 4d), with a dorsal lobe or swelling representing a dorsal cirrus, without ventral cirrus. Setae of four kinds: dorsal to acicula 1-3 thin gradually tapering capillary setae (Fig. 4e) and 1-2 somewhat shorter blunt distally dilated capillary setae (Fig. 4f), ventral to acicula 3-6 compound setae with blunt-tipped blades (Fig. 4g) and one needle-thin slightly curved unjointed inferior seta emerging from the tip of the setal lobe (Fig. 4h). Compound setae with blades of about equal lengths. Mandibles moderately chitinized, each piece with four distinct teeth (Fig. 4b). Maxillae of p-type, with 8 pairs of denticles in two rows, posterior small pieces ('forceps') weakly fused (Fig. 4c).

Source : MNHN, Paris

REMARKS. — This form is close to *Ophryotrocha littoralis* (Levinsen, 1879), which is the only *Ophryotrocha* species hitherto described having mandibles with four strong teeth (Fig. 4i). It seems to differ from it in having a smaller size, in the shape of the palps, and in details of dentition of the maxillary parts. The mandibles are

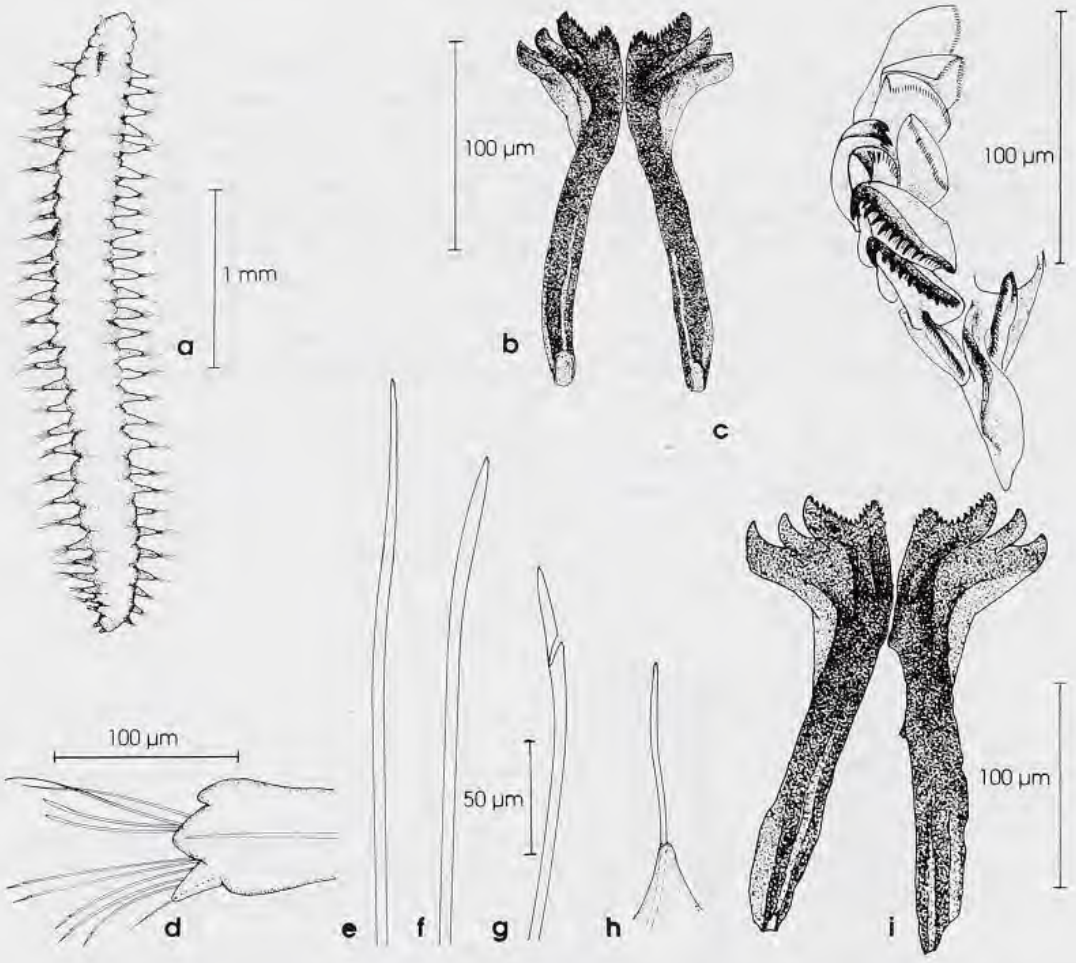



FIG. 4. — *Ophryotrocha* sp: **a**, complete specimen, dorsal view. **b**, mandibles. **c**, maxillae, forceps and left denticle row. **d**, parapodium, setiger 10. **e**, **f** supra-acicular simple setae. **g**, subacicular compound seta. **h**, inferior simple seta. *Ophryotrocha littoralis*: **i**, mandibles.

strikingly similar, but are smaller than in *O. littoralis* (Figs 4b, i). The specimens may belong to a new species, but the material at hand was considered insufficient for naming a new species.

The type collection of *O. littoralis* (= *Paractius littoralis*) contains numerous specimens which all are well preserved. Most characters are referred to in the original description (LEVINSEN, 1879), but the figures fail to show critical details of jaw parts. The palps appear shorter than originally stated.

## ACKNOWLEDGEMENTS

Part of this work was performed during a stay at the Zoological Museum of Copenhagen. I am indebted to Mary E. PETERSEN (ZMUC) for invaluable help during the stay, for arranging the loan of type specimens of *O. littoralis*, and for suggestions to the manuscript. Alexander TZETLIN, University of Moscow, and Danny E. JACOBSEN (ZMUC) provided and translated Russian literature. I also wish to thank the skipper of R/V 'Ottar' Kåre Bendiksen for assistance during sampling and Pat DINEEN and Synnøve LASSEN for language corrections.

Source : MNHN, Paris

## REFERENCES

ÅKESSON, B., 1973. — Reproduction and larval morphology of five *Ophryotrocha* species (Polychaeta, Dorvilleidae). *Zool. Scripta*, **2** : 145-155.

ÅKESSON, B., 1984. — Speciation in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae). *Fortschr. Zool.*, **29** : 299-316.

AVERINCEV, V.G., 1989. — *Seasonal dynamics of polychaetes from the high Arctic coastal ecosystem of Franz-Joseph Land (Errantia).* (In Russian). Akademya NAUK, SSSR.

FAUVEL, P., 1923. — Polychètes errantes. *Faune Fr.*, **5** : 1-488.

FOURNIER, J.A. & CONLAN, K.E., 1994. — A new species of *Ophryotrocha* (Polychaeta; Dorvilleidae) associated with ice scours in the Canadian Arctic Archipelago. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 185-190.

GEORGE, J.D. & HARTMANN-SCHRÖDER, G., 1985. — Polychaetes: British Amphinomida, Spintherida and Eunicida. *Synop. Brit. Fauna*, **32** : 1-221.

HARTMANN-SCHRÖDER, G., 1971. — Annelida, Borstenwürmer, Polychaeta. *Tierwelt Dtl.*, **58** : 1-594.

HILBIG, B. & BLAKE, J.A., 1991. — Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with a generic revision of *Ophryotrocha*. *Zool. Scr.*, **20** : 147-183.

LA GRECA, M., & BACCI, G., 1962. — Una nuova specie di *Ophryotrocha* delle coste tirreniche *(Annelida, Polychaeta)*. *Boll. Zool.*, **29** : 7-18.

LEVINSEN, G.M.R., 1879. — Om to nye Slægter af arctiske chætopode Annelider. *Vidensk. Meddel. nat. Foren.* 1879 (Denmark) : 9-18.

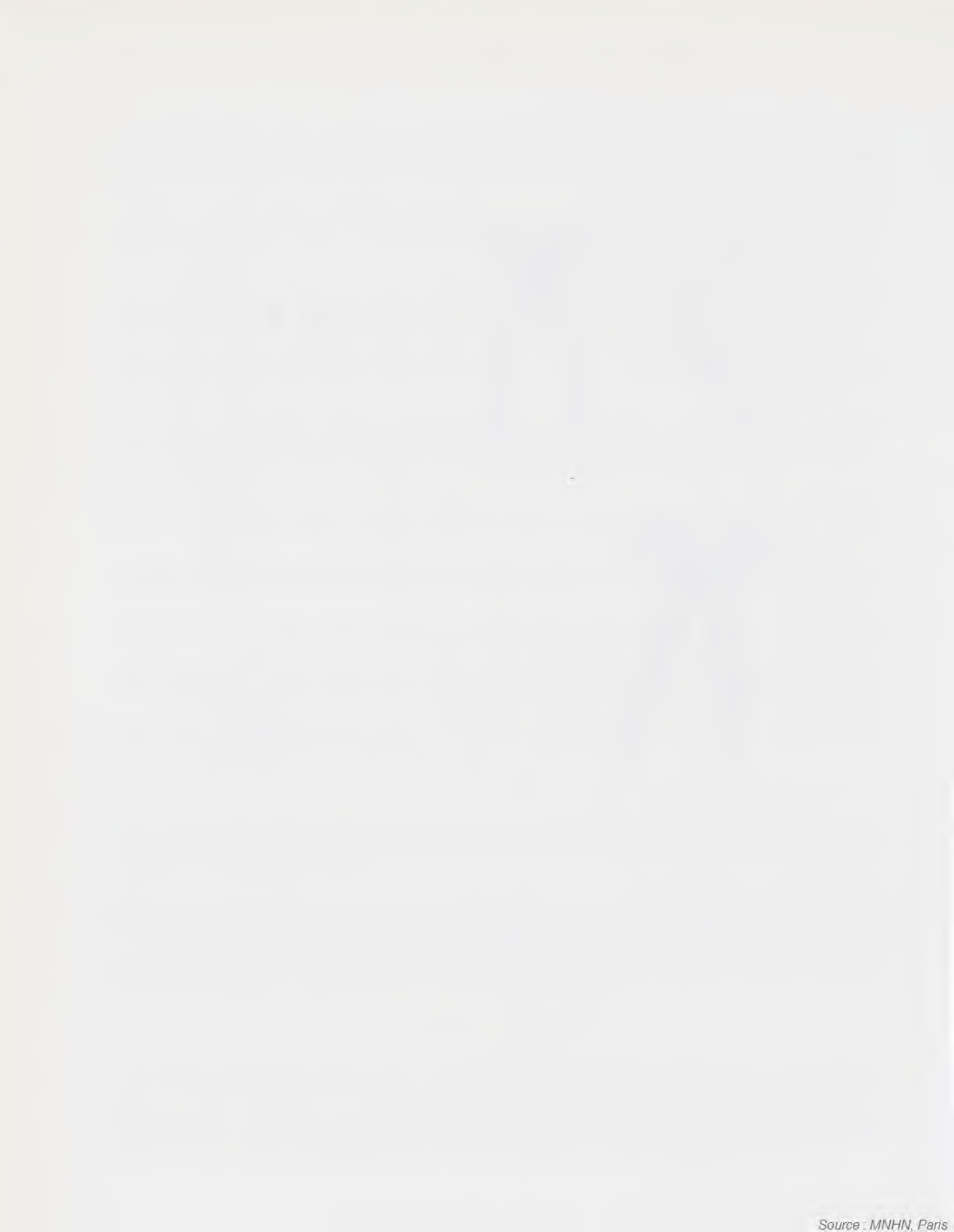
ORENSANZ, J.M., 1990. — The eunicemorph polychaete annelids from Antarctic and subantarctic seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the southern Indian Ocean. *Antarct. Res. Ser.*, **52** : 1-183.

OUG, E., 1990. — Morphology, reproduction, and development of a new species of *Ophryotrocha* (Polychaeta: Dorvilleidae) with strong sexual dimorphism. *Sarsia*, **75** : 191-201.

OUG, E., LEIN, T.E., HOLTE, B., ORMEROD, K. & NÆS, K., 1985. — *Basisundersøkelse i Tromsøsund og Nordbotn 1983. Fagrapport.* SFT/NIVA report 173b/84 (In Norwegian). Oslo, 160 pp.

PARENTI, U., 1961. — *Ophryotrocha puerilis siberti, O. hartmanni* ed *O. baccii* nelle acque di Roscoff. *Cah. Biol. mar.*, **2** : 437-445.

Source : MNHN, Paris



Source : MNHN, Paris

# Distributional patterns and taxonomic notes on Lumbrineridae from Crete (S. Aegean, Eastern Mediterranean)

*K.-Nadia PAPADOPOULOU, C. DOUNAS & Chris J. SMITH*

Institute of Marine Biology of Crete
P.O. Box, 2214, 71003 Iraklio, Crete, Greece

ABSTRACT

Lumbrineridae were collected from soft sediment at 11 coastal and shelf areas from the island of Crete. Collections were made at 182 stations ranging in depth from 10 to 330 m. Eleven species were found. Three species were common and present throughout the area. Of these, *Lumbrineris gracilis*, was by far the most abundant species at depths down to 130 m. This species was one of the 10 most dominant macrofaunal species between 40 and 70 m depth. *Lumbrineris nonatoi* was the second most abundant species at stations down to 70 m. *Scoletoma emandibulata mabiti* was found in lower numbers than *L. gracilis* at all depths but was recorded from a wider depth range (10-330 m). *Lumbrinerides* sp. A is new for the Mediterranean and its relationship to other species of the genus is discussed.

RÉSUMÉ

**Modèles de distribution et notes taxonomiques sur les Lumbrineridae de Crète (Sud de la mer Égée, Méditerranée orientale)**

Des Lumbrineridae provenant des sédiments meubles ont été collectés parmi 11 zones de la côte et de la marge continentale tout autour de l'île de Crète, comprenant 182 stations situées à des profondeurs variant entre 10 et 330 mètres. Onze espèces ont été trouvées parmi lesquelles trois espèces étaient présentes sur toutes les zones de l'étude. *Lumbrineris gracilis* était l'espèce la plus abondante à toutes les profondeurs jusqu'à 130 mètres. Entre 40 et 70 mètres, *L. gracilis* était une des 10 espèces les plus dominantes de la macrofaune. *Lumbrineris nonatoi* était la deuxième espèce la plus abondante de toutes les stations peu profondes jusqu'à 70 mètres. *Scoletoma emandibulata mabiti* était moins abondante que *L. gracilis*, à toutes les profondeurs mais a été enregistrée dans une plus grande gamme de profondeurs (10-330 m). *Lumbrinerides* sp. A est une nouvelle espèce pour la Mediterranée et sa relation avec d'autres espèces du même genre est discutée.

## INTRODUCTION

Our knowledge of the Eastern Mediterranean polychaete fauna is limited. Only a small number of papers on

PAPADOPOULOU, K.N., DOUNAS, C. & C.J. SMITH, 1994. — Distributional patterns and taxonomic notes on Lumbrineridae from Crete (S. Aegean, Eastern Mediterranean). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 259-268. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

ecology or taxonomy have been published to date. None of these were concerned with the Lumbrineridae. The family Lumbrineridae has been extensively investigated in a number of areas worldwide (HARTMAN, 1965; DAY, 1967; FAUCHALD, 1970; ORENSANZ, 1973, 1990; PERKINS, 1979; UEBELACKER, 1984; IMAJIMA, 1985; GEORGE & HARTMANN-SCHRÖDER, 1985; FRAME, 1992). Up to 13 genera are now recognized in the family, including the recent additions of *Abyssoninoe* Orensanz, 1990, *Eranno* Kinberg, 1865, *Lumbricalus* Frame, 1992, and *Scoletoma* Blainville, 1828. Over 200 species have been described in the family and more are being added (UEBELACKER, 1984). In the Mediterranean, seven genera and approximately 20 species have been recorded. Information concerning this family in the region has been provided by BEN-ELIAHU (1976), RAMOS (1976), CAMPOY (1979) and MIURA (1980) and records have also appeared in a number of benthic species lists (CARPINE, 1970; FREDJ, 1974; SALEN-PICARD, 1982). Previous listings of Lumbrineridae may also include some misidentified species.

The study by RAMOS (1976) remains the most authoritative work for the Mediterranean, but is restricted to the Western Mediterranean from the Spanish Catalan coast to the Adriatic Sea. There is a large gap in the information concerning the Aegean area, in particular the Southern Aegean and the area around Crete. This is an important geographical region where several water masses meet, including from the Atlantic, the Levantine Basin (allowing for passage of Lesseptian migrants), the Libyan Sea, the Ionian sea and influences from the Black Sea through the Sea of Marmara and the Aegean. The present study investigates the family Lumbrineridae from around the island of Crete over a range of different sediment types and depths.

## METHODS AND MATERIALS

Soft bottom lumbrinerid polychaetes were collected from 11 coastal and shelf areas from around the island of Crete during several quantitative benthic faunal surveys carried out from 1987 to 1989 (Fig. 1). These were pilot surveys for the most part. In all, 182 stations were sampled at depths ranging from 10 to 330 m. Most of the stations were along transects at standard depths of 10, 20, 30, 40, 70, 100, 130, 160 and 190 m. Samples were taken using a Smith-McIntyre grab (0.1 $m^2$). One macrofaunal grab per station was analysed and four undisturbed cores were taken from an additional grab for physico-chemical measurements. Macrofaunal samples were immediately mixed into a sea water slurry and washed through a 0.5-mm sieve. The residues were transferred to containers and fixed with 10 % buffered formalin. In the laboratory Rose Bengal was added and after 24 hours the samples were washed with freshwater and screened again through a 0.5-mm mesh size sieve. The stained fauna was then sorted to major taxa and preserved in 4 % buffered formalin prior to identification to species. The material is deposited at the Institute of Marine Biology of Crete.

## STUDY AREAS

The north coast of Crete, where most of the stations were situated, has a generally consistent sedimentary environment which grades from coarse sands on the beaches to fine silty clays in deeper areas. Exceptions to this are: the western part of Rethymnon Bay where the sediment at 20-40 m depth is much coarser with high biogenic detritic content; the enclosed Bay of Souda (which physically resembles a fjord) where sediments are generally finer; and Mirambelo Bay which has a central shallow seamount where the sediment is coarser and of biogenic detritic origin.

The south coast, which has rocky shores with only a few bays, is much steeper and the width of the continental shelf is consequently much narrower. Messara and Ierapetra Bays, however, slope away more gently in front of open valleys. At Kali Limenes Bay the sediment is gravelly sand with pebbles at 10-20 m depth and retains a large coarse fraction as far down as 100 m. At the South East stations, the sediment is of biogenic detritic origin and contains calcareous algal fragments.

Biologically, the Cretan coastal sedimentary environment is characterized by seagrasses from 10 to 25 m depth and the alga *Caulerpa prolifera* from 25 to 40 m. At 70 m, numerous dead *Turritella* and, to a lesser extent, *Dentalium* shells are inhabited by hermit crabs and sipunculids. Below this, the environment is rather featureless except in terms of microtopography caused by the bioturbatory activities of burrowing animals. The benthic infauna is characterised by the presence of *Ditrupa arietina* at 30 to 40 m and *Amphiura chiajei* and *A. filiformis* below 50 m. The crinoid *Leptometra phalangium* is present in very high numbers from 130 to 200 m depth (predominantly on the north coast).

Source : MNHN, Paris

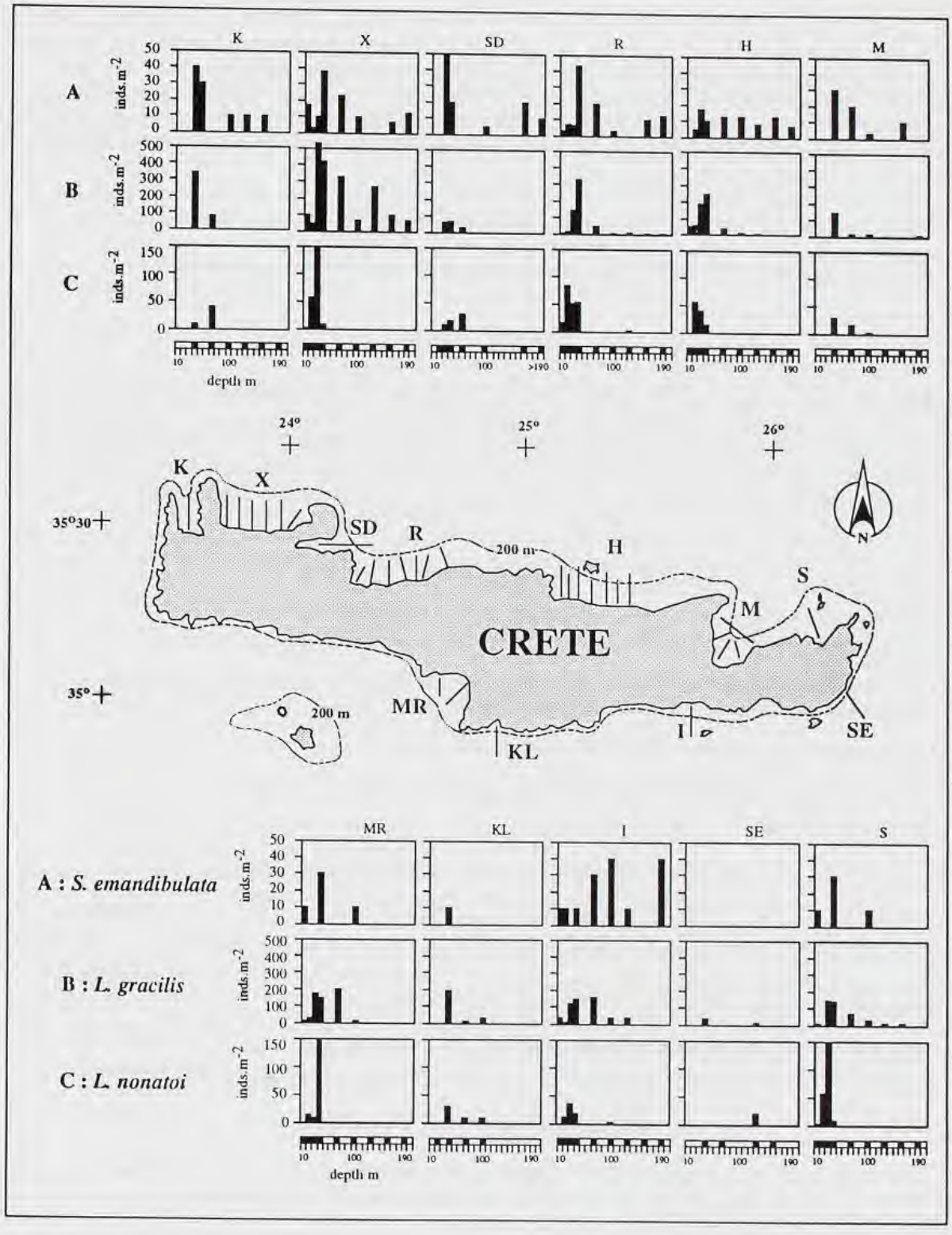



FIG. 1. — Crete. Sampling stations (K: Kissamos, X: Chania, SD: Souda, R: Rethymnon, H: Iraklio, M: Mirambello, S: Sitia, SE: South East, I: Ierapetra, KL : Kali Limenes, MR : Messara). Average depth distribution of *S. emandibulata mabiti* (a), *L. gracilis* (b) and *L. nonatoi* (c) for each of the study areas.

Source : MNHN, Paris

## RESULTS

A total of 1999 lumbrinerids was found and the following 11 species have been identified: *Lumbrineris coccinea* (Renier, 1804), *L. gracilis* (Ehlers, 1868), *L. latreilli* (Audouin & Milne Edwards, 1834), *L. nonatoi* Ramos, 1976, *Scoletoma emandibulata mabiti* (Ramos, 1976), *S. funchalensis* (Kinberg, 1865), *S. fragilis* (O.F. Müller, 1776), *S. impatiens* (Claparède, 1868), *Ninoe armoricana* (Glémarec, 1968), *Lumbrineriopsis paradoxa* (de Saint-Joseph, 1888) and *Lumbrinerides* sp. A. Presence-absence data for all the species found, number of stations and depth ranges investigated per sampling area are given in Table 1.

*Lumbrineris gracilis*, *L. nonatoi* and *S. emandibulata mabiti* were the numerically dominant species. Abundances for these three species were such that their average depth distribution could be plotted for each of the study areas (Fig. 1). All three species were found in all locations except for *L. gracilis* and *S. emandibulata mabiti* in the South East (transect SE) stations. Distributions for each of these species are discussed below.

## SPECIES NOTES

According to the latest revision of FRAME (1992) the genus *Lumbrineris* Blainville, 1828 has been restricted to species with composite hooks, simple hooks and simple limbate setae; the genus *Scoletoma* de Blainville, 1828 has been resurrected to include species with simple hooks and simple limbate setae and the genus *Lumbricalus* Frame, 1992 has been erected to include species with composite spinigers, composite hooks, simple hooks and simple limbate setae. Based on this division, the following keys are given for the Cretan species.

Key to the species of *Lumbrineris* de Blainville, 1828

| | | |
|---|---|---|
| 1 | Elongated parapodial lobes in posterior body region. Mx III bidentate | **2** |
| | Not elongated parapodial lobes in posterior body region. Mx III unidentate | **3** |
| 2 | Presetal parapodial lobes longer than postsetal lobes. Mx II = 3 | *L. nonatoi* |
| | Presetal parapodial lobes smaller than postsetal lobes. Mx II > 3 | *L. gracilis* |
| 3 | Prostomium round, globular. Blades of composite hooks of similar length throughout | *L. coccinea* |
| | Prostomium conical. Blades of composite hooks longer in anterior parapodia | *L. latreilli* |

Key to the species of *Scoletoma* de Blainville, 1828

| | | |
|---|---|---|
| 1 | Limbate setae with terminal hook in the first anterior parapodia | *S. emandibulata mabiti* |
| | No such setae | **2** |
| 2 | Prostomium broadly rounded. Aciculae amber | *S. funchalensis* |
| | Prostomium conical | **3** |
| 3 | Aciculae yellow. Hooks starting on setiger 1-5 | *S. impatiens* |
| | Aciculae black. Hooks starting on setiger 22-35 | *S. fragilis* |

### *Lumbrineris gracilis* (Ehlers, 1868)

*Lumbriconereis gracilis* Ehlers, 1868 (type locality Fiume, Adriatic) — FAUVEL, 1923 : 432, fig. 172 a-f.
DISTRIBUTION. — Mediterranean, Black Sea, N. Atlantic, North Sea, intertidal to about 680 m depth.

*L. gracilis* has always presented problems as to its identification (SALEN-PICARD, 1982). Some authors would refer to a *L. gracilis-latreilli* complex rather than separating these two species (AMOUREUX, 1987). Apart from the differences used to distinguish the two species, such as the shape of the prostomium and the length of the compound setae, RAMOS (1976) utilised the presence (*L. gracilis*) or absence (*L. latreilli*) of elongated parapodial

Source : MNHN, Paris

lobes in the posterior body region. The number of anterior parapodia with compound hooked setae can also be used to separate *L. gracilis* (10-15) from *L. latreilli* (20-30) (GEORGE & HARTMANN-SCHRÖDER, 1985). However this is probably only applicable to adults.

*L. gracilis* was by far the most abundant species (60 % of the lumbrinerid individuals), found at 117 of the 182 stations, on various combinations of gravel, sand, mud, clay, maërl and biogenic detritus, from 10 to 190 m. Highest abundances were recorded between 30 and 70 m where *L. gracilis* was one of the 10 most abundant macrofaunal species. The maximum abundance observed for *L. gracilis* was 910 ind. $m^{-2}$ at a 40-m sandy silt station in Chania Bay.

### *Lumbrineris nonatoi* Ramos, 1976

*Lumbrineris nonatoi* Ramos, 1976: 124, figs 19-21 (type locality: Rosas Bay, Spanish Catalan coasts).
DISTRIBUTION. — Mediterranean, from 10 to 130 m.

*L. nonatoi* was originally described from a "sandy mud polluted bottom" at 10 m depth (RAMOS, 1976) from the Spanish Catalan coast. Since then, there have been very few records of *L. nonatoi* from the Aegean or the Eastern Mediterranean. Our findings agree well with Ramos' (1976) description. *L. nonatoi* is a very distinct but minute species: prostomium conical, slightly wider than long, composite multidentate and very short hooded hooks from setiger 1, Maxillae II with three teeth each, posterior parapodia with elongated presetal lobes, longer than postsetal lobes. It seems that *L. nonatoi* is fairly common in the Aegean, but because of its small size, it may have been misidentified as juvenile *L. gracilis*.

*L. nonatoi* was the second most abundant species (25 % of the lumbrinerid individuals, present at 69 of the 182 stations). The species prefers coarse sand or shelly bottoms, but was generally found in sand, mud, gravel, and various combinations of these, from 10 to 130 m. Large numbers were recorded from 20 to 40 m, dropping sharply at 70 m. At 20 m the mean abundance was slightly higher than that of *L. gracilis*. The highest abundance recorded for *L. nonatoi* was 370 ind. $m^{-2}$ at a 30-m sandy station in Ierapetra Bay, on the south coast, while the maximum average (round Crete average calculated for each depth class) abundance, found at 40 m, was only 81 ind. $m^{-2}$.

*L. nonatoi* had maximum abundances in Sitia, Messara and Chania Bay at 30-40 m depth. *L. nonatoi* has a similar distributional pattern to *L. gracilis*, with maximum abundances at 40 m. It did not extend into as deep waters as *L. gracilis*.

### *Lumbrineris latreilli* Audouin & Milne Edwards, 1834

*Lumbrineris latreilli* Audouin & Milne Edwards, 1834 (type locality: France).
*Lumbriconeris latreilli* : FAUVEL, 1923: 432, fig. 171 m-r.
DISTRIBUTION. — A cosmopolitan species (Greenland, Norway, Iceland to France, Mediterranean, Gulf of Mexico, Indian Ocean, Red Sea, Japan, West and South Africa), in temperate and warm waters from 10 to 2,000 m.

There has been much discussion on how to separate *L. latreilli* and *L. coccinea*. FRAME (1992) introduced the use of the length of blades of the composite hooks.

A few specimens of *L. latreilli* were found at only two stations, in mixed substrates at 30-40 m depth. It has frequently been reported from the Aegean and the Ionian Sea (HARMELIN,1969; BOGDANOS & SATSMADJIS, 1987; DOUNAS & KOUKOURAS, 1992); it has probably been occasionally confused with *L. gracilis*. It is usually found in coastal coarse sands and *Ditrupa* sands (GLÉMAREC, 1969).

### *Lumbrineris coccinea* (Renier, 1804)

*Nereis coccinea* Renier, 1804 (type locality: Mediterranean).
*Lumbriconeris coccinea:* FAUVEL, 1923: 432, fig. 172 g-n.
DISTRIBUTION. — outside the Mediterranean, *L. coccinea* has been found in the Atlantic, North Pacific, South Africa, Red Sea and Indian Ocean, from the intertidal zone to 1,268 m depth.

Source : MNHN, Paris

*L. coccinea* and *L. latreilli* can be separated as shown in the key above. The shape of Maxillae III can also be used to distinguish *L. coccinea* (Maxillae III: B+B, with two "expansions aliformes non dentelées ") from *L. latreilli* (Maxillae III: A2+A2, with one "expansion aliforme bidentée") (MIURA, 1980).

A single specimen of *L. coccinea* was found at a gravelly sand station, on the north coast, at 40 m depth. In the Mediterranean it is known to occur frequently in higher numbers in "coralligène" substrates (BELLAN, 1964).

### *Scoletoma emandibulata mabiti* (Ramos, 1976)

*Lumbrineris emandibulata mabiti*: RAMOS, 1976: 112, figs 7-10 (type locality: Rosas Bay, Spanish Catalan coast).
DISTRIBUTION. — Mediterranean, from 6 to 330 m.

There are very few previous records of *S. emandibulata mabiti* from the Aegean or the Eastern Mediterranean (DOUNAS & KOUKOURAS, 1992). This is surprising because *S. emandibulata mabiti*, is also well described and distinctive: prostomium conical, longer than wide, simple limbate setae with terminal hook in the first anterior parapodia, which are gradually replaced by simple pluridentate hooded hooked setae, Maxillae II with four teeth and Maxillae III with two teeth each.

*S. emandibulata mabiti* was the third most abundant species (10 % of individuals). It was present at 94 of the 182 stations, from 10 to 330 m depth. *S. emandibulata mabiti* occurred in a variety of mixed substrates but had its higher numbers in fine silty sediments. The bathymetric distribution given by RAMOS (1976) (6 to 295 m) for the Western Mediterranean is essentially within the same depth range. Abundances were generally low throughout the area, lower than *L. nonatoi* at the shallow depths and *L. gracilis* at the deeper stations. Maximum numbers of 140 ind. $m^{-2}$ were recorded at a 40 m silty station in Rethymnon Bay.

*S. emandibulata mabiti* had its maximum numbers in the North West stations, at 40 m depth in Souda and Rethymnon Bays and at 70 to 190 m in Ierapetra Bay, in the South. In terms of distributional patterns, Ierapetra Bay was an exception as the maximum abundances were found at depths below 40 m. This is perhaps due to localised enrichment which was reflected in a slightly modified macrofaunal community.

*S. emandibulata mabiti*, has the same distributional pattern as *L. gracilis* but with a wider depth range and significantly lower numbers.

### *Scoletoma impatiens* (Claparède,1868)

*Lumbriconereis impatiens* Claparède, 1868 (type locality: Cape of Good Hope, South Africa) — FAUVEL, 1923: 429, fig. 171 a-i.
DISTRIBUTION. — A cosmopolitan species. Atlantic, Mediterranean, Indian Ocean, Red Sea, South West Africa, from the intertidal zone to a depth of approximately 2500 m.

Thirteen specimens of *S. impatiens* were found at 9 stations around Crete, from 20 to 160 m, in sand, mud, broken shell, gravel and mixed bottoms. *S. impatiens* has frequently been reported from both the Western and the Eastern Mediterranean. It is often confused with *S. emandibulata mabiti* (SALEN-PICARD, 1982) since they are very similar in appearance. Both have a sharply conical prostomium but *S. emandibulata mabiti* has simple limbate setae with a terminal hook in the first anterior parapodia and *S. impatiens* has simple hooded hooked setae starting on setigers 1-5.

### *Scoletoma fragilis* (O.F. Müller, 1766)

*Lumbricus fragilis* O.F. Müller, 1766 (type locality: Denmark)
*Lumbriconeris fragilis*: FAUVEL, 1923: 432, fig. 171 k-l.
DISTRIBUTION. — Mediterranean, N. Atlantic, N. Pacific, North Sea, Bering Sea, Japan, from the intertidal zone to 3,500 m depth.

*S. fragilis* was found at a single fine silt station (two specimens), off the north coast, at 130 m depth, in Iraklio Bay. *S. fragilis* can easily be separated from *S. impatiens* and *S. funchalensis* by the presence of black aciculae.

It has been reported from sand, mud, gravel and various combinations of these, and among *Posidonia* meadows (GEORGE & HARTMANN-SCHRÖDER, 1985). It is commonly found in coastal coarse sands and gravel from atlantic french coasts (GLÉMAREC, 1969).

Source : MNHN, Paris

### *Scoletoma funchalensis* (Kinberg, 1865)

*Lumbriconereis funchalensis* Kinberg, 1865 (type locality: Madeira), FAUVEL, 1923: 434, fig. 172 o-r.
DISTRIBUTION. — Mediterranean and Atlantic, to about 100 m depth.

*S. funchalensis*, along with *S. impatiens* and *S. fragilis*, lacks compound hooded hooked setae. The first 12-20 anterior parapodia with winged capillary setae and simple hooded hooked setae with the remaining parapodia with only simple hooded hooked setae. Aciculae amber coloured.

*S. funchalensis* was found at only two stations in Iraklio Bay, in very low densities at 20 and 30 m depth, in coarse sands with broken shell. *S. funchalensis* has been previously recorded in association with the sponges in the North Aegean (VOULTSIADOU-KOUKOURA *et al.*, 1987).

### *Ninoe armoricana* Glémarec, 1968

*Ninoe armoricana*: GLÉMAREC, 1968: 315, fig. 1-4, (type locality: North Bay of Biscay, continental shelf), RAMOS, 1976: 130, figs 24-26.
DISTRIBUTION. — North Eastern Atlantic, Mediterranean, from 6 to 330 m depth.

VAMVAKAS (1970) found one specimen of *Ninoe kinbergi* Ehlers, 1887 in Iraklio Bay at 330 m depth. This record, which is the only record of *N. kinbergi* from the Eastern Mediterranean, may have been misidentified. We believe that the Aegean form is closer to *N. armoricana* Glémarec, 1968 rather than to *N. kinbergi* or *N. nigripes* Verrill, 1873 *sensu* PETTIBONE (1963).

Only 10 individuals were found on the north coast of Crete; at four stations in Souda Bay, in fine silty sediments, at 95-265 m depth and at a single station in Iraklio Bay at 160 m. In the Eastern Mediterranean, *N. armoricana* was previously recorded from the North Aegean, in high densities at 50-70 m depth (DOUNAS & KOUKOURAS, 1992).

### *Lumbrineriopsis paradoxa* (de Saint-Joseph, 1888)

*Lumbriconereis paradoxa* de Saint-Joseph, 1888, ? FAUVEL, 1923 : 434, fig. 173 a-h.
*Lumbriconereis mucronata* Ehlers, 1908, ORENSANZ, 1973: 377, fig. XIII.
*Lumbrineris paradoxa* Harmelin, 1964
*Lumbrineriopsis paradoxa* ORENSANZ, 1973: 375, not GARDINER, 1976: 205, fig. 26 m-o.
DISTRIBUTION. — Mediterranean, West Africa, Azores, Bermuda, N. Carolina, Mexico from 10 to 1,700 m depth.

This species has received much attention as to the specimens ascribed and to its synonymy with *L. nucronata*. RAMOS (1976) criticized the synonymy with *L. mucronata* and discussed a Mediterranean form *Lumbrineris* cf *paradoxa*. This later species has one peristomial ring and short mandibles with denticulate margin which has been observed in all previous collections from the Mediterranean and also from this study. These characters have also been observed from specimens from Bermuda (HARTMAN, 1965) and from the Gulf of Mexico (UEBELACKER, 1984). MIURA (1980) in his revision of the genus introduced the use of the shape of the prostomium and the colour of the aciculae. He described *Lumbrineriopsis gardineri* from Gardiner's (1976) "*L. paradoxa*" material. It seems that some confusion still exists and further work is required.

Only a few specimens were found at 16 of the 182 stations in coarse sediments such as "*Amphioxus* sands" at depths from 20 to 160 metres. Mean abundance ranged from 2 to 4 ind. $m^{-2}$ with maximum abundance at 40 m. Known previously from the Ionian Sea (BOGDANOS & SATSMADJIS, 1987) and the North Western Mediterranean (BELLAN, 1964; RAMOS, 1976).

### *Lumbrinerides* sp. A

MATERIAL EXAMINED. — Kali Limenes, seven specimens at 16 m depth; Chania Bay, 5 specimens at 20 and 30 m depth; and Rethymnon Bay, eight specimens at 20-40 m. Found in coarse sediments such as "*Amphioxus* sands", coarse sands with shell fragments and gravelly sand.

The body is long and slender and the prostomium is elongate, conical without eyes or eye spots. The peristomium is composed of two equally long rings. Maxillae I with 2 weakly developed small accessory teeth each, Maxillae II with three round teeth each, Maxillae III dentate subrectangular plates and Maxillae IV cup shaped

Source : MNHN, Paris

oval plates. Maxillary carriers triangular, darker than rest of maxillae. Mandibles Y-shaped, light brown. First 6-7 anterior parapodia minute, with very small setal lobes, increasing in size from the 8th setiger. They reach their maximum length at setiger 12-13 and from setiger 22 onward they decrease in size. The setae include simple hooded hooks from the first setiger, broadly limbate setae and two pale pointed aciculae. The pygidium is typical for the genus.

*Lumbrinerides* sp. A differs from the other Mediterranean species of the genus: *L. carpinei* (Ramos, 1976) which has one accessory tooth in Maxillae I, one very long peristomial ring and only three minute anterior parapodia, and *Lumbrinerides* sp. (RAMOS, 1976) (originally identified by RAMOS as *Lumbrineris acuta*) which has no accessory tooth in Maxillae I and simple hooded hooks from the 16th setiger.

*Lumbrinerides* sp. A will be described in the near future by us after a revision of the Mediterranean members of the family and further examination of type material and material from other localities.

## DISCUSSION

In considering the biogeographical origins of the Cretan Lumbrinerids, three groups can be identified. The first is the cosmopolitan species, *Lumbrineris latreilli*, *L. coccinea*, *Scoletoma impatiens* and *S. fragilis*. These have a world wide distribution from the Atlantic through the Mediterranean and Red Sea to the Indian and Pacific Oceans. The second group includes the Atlanto-Mediterranean species, *Lumbrineris gracilis*, *Ninoe armoricana* and *Lumbrineriopsis paradoxa*. These are probably of Atlantic origin, which have penetrated the Mediterranean and, in the case of *L. gracilis*, the Black Sea. The last group is the Mediterranean endemic species, *L. nonatoi* and *S. emandibulata mabiti*. No lessepsian migrants have been recorded from the Red Sea. The probable explanation for the recorded distributions are probably due to factors such as the depth range of the species, dispersive current patterns and the temperature and salinity extremes in the Mediterranean and Red Sea.

TABLE 1. — Occurrence of species, depths sampled and number of stations per sampling area

| | SAMPLING AREAS (See Fig. 1 for location) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | K | X | SD | R | H | M | S | SE | I | KL | MR |
| Number of stations | 6 | 35 | 13 | 39 | 40 | 12 | 9 | 4 | 9 | 4 | 11 |
| Depths sampled (in m) | 16-100 | 10-190 | 25-330 | 10-190 | 10-190 | 40-190 | 10-190 | 10-100 | 10-190 | 10-100 | 10-190 |
| Species | | | | | | | | | | | |
| *Lumbrineris gracilis* | * | * | * | * | * | * | * | * | * | * | * |
| *L. nonatoi* | * | * | * | * | * | * | * | * | * | * | * |
| *L. latreilli* | | | | | * | | | | | * | |
| *L. coccinea* | | | | | | | * | | | | |
| *Scoletoma emandibulata mabiti* | * | * | * | * | * | * | * | | * | * | * |
| *S. funchalensis* | | | | | * | | | | | | |
| *S. impatiens* | | * | | * | * | | | | | * | |
| *S. fragilis* | | | | | * | | | | | | |
| *Ninoe armoricana* | | | * | | * | | | | | | |
| *Lumbrineriopsis paradoxa* | | * | | * | * | * | * | * | * | * | |
| *Lumbrinerides* sp. A | | * | | * | | | | | | * | |

## ACKNOWLEDGEMENTS

This work constitutes part of the NATO Science for Stability GR-FISHECO project. The organisational and financial help from SFS is gratefully acknowledged and much appreciated. We are particularly grateful to

Source : MNHN, Paris

Dr I. KARAKASSIS, IMBC, for access to his Thesis material and to Dr. M. PETERSEN, Zoological Museum, University of Copenhagen, for critically reading an earlier draft of this manuscript.

## REFERENCES

AMOUREUX, L., 1987. — Annélides polychètes du talus continental européen. Données complémentaires concernant les campagnes 1970-1971-1972 de la "Thalassa". Données globales sur l'ensemble des six campagnes (1967 à 1973). *Cah. Biol. mar.*, **28** : 569-577.

BELLAN, G., 1964. — Campagne de la Calypso : Méditerranée nord-orientale. 6. Annélides Polychètes. *Ann. Inst. océan.*, **41** : 271-288.

BEN-ELIAHU, M.N., 1976. — Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the gulf of Elat: Sedentaria. *Isr. J. Zool.*, **25** : 121-155.

BOGDANOS, C., & J., SATSMADJIS, 1987. — The Patraikos bottom Fauna. *Thalassographica*, **10** : 37-71.

CAMPOY, A., 1979. — Lista de especies de Anélidos Poliquetos conocidas de las costas de la Peninsula Ibérica. *Inv. Pesq.*, **43** : 737-767.

CARPINE, C., 1970. — Écologie de l'étage bathyal dans la Méditerranée occidentale. *Mém. Inst. océanogr., Monaco*, **2**, 146 pp.

DAY, J.H., 1967. — A monograph on the polychaeta of the Southern Africa. Part. 1: Errantia. *Trust. Brit. Mus. (Nat. Hist.)*, **656** : 1-458 pp.

DOUNAS, C., & A., KOUKOURAS, 1992. — Circalittoral macrobenthic assemblages of Strymonikos Gulf (N. Aegean Sea). *P.S.Z.N.I.: Mar. Ecol.*, **13** : 95-99.

FAUCHALD, K., 1970. — Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from western Mexico. *All. Hanc. Monogr. Mar. Biol.*, **5** : 1-335.

FAUVEL, P., 1923. — Polychètes errantes. *Faune Fr.*, **5** : 1-488.

FRAME, A.B., 1992. — The Lumbrinerids (Annelida: Polychaeta) collected in two northwestern Atlantic surveys with descriptions of a new genus and two new species. *Proc. biol. Soc. Wash.*, **105** : 185-218.

FREDJ, G., 1974. — *Essai de stockage et d'exploitation des données en écologie marine*. Thèse Doct. Etat Sciences naturelles, Univ. Nice, 176 pp.

GARDINER, S.L., 1976. — Errant polychaete annelids from North Carolina. *Elisha Mitchell Sci. Soc.*, **91** : 77-220.

GEORGE, J.D., & G. HARTMAN-SCHRÖDER, 1985. — Polychaetes: British Amphinomida, Spintherida and Eunicida. Keys and notes for the identification of the species. *Synop. Brit. Fauna*, **32** : 1-227.

GLÉMAREC, M., 1968. — *Ninoe armoricana* n.sp., polychète Lumbrineridae de la "Grande Vasière" (Golfe de Cascogne). *Vie Milieu*, **19** : 315-322.

GLÉMAREC, M., 1969. — *Les peuplements benthiques du plateau continental nord-Gascogne*. Thèse Doct. État Sciences naturelles, Univ. Paris, 167 pp.

HARMELIN, J.G., 1969. — Contribution à l'étude de l'endofaune des prairies d'*Halophila stipulacea* de Méditerranée orientale. I. Annélides, Polychètes. *Rec. Trav. St. Mar. Endoume*, **45** : 305-316.

HARTMAN, O., 1965. — Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Found. Publ. Occas. Pap.*, **28** : 1-378.

IMAJIMA, M., 1985. — Six species of *Lumbrinerides* (Polychaeta, Lumbrineridae) from Japan. *Bull. natn. Sci. Mus.*, Tokyo, ser.A, **11** : 171-184.

MIURA, T., 1980. — Lumbrineridae (Annélides Polychètes) abyssaux récoltés au cours de campagnes du Centre Océanologique de Bretagne dans l'Atlantique et la Méditerranée. *Bull. Mus. natn. Hist. nat.*, Paris, 4e sér., **2A** : 1019-1057.

ORENSANZ, J.M., 1973. — Los anélidos poliquetos de la provincia biogeografica Argentina. IV. Lumbrineridae. *Physis Secc. A.*, Buenos Aires, **32** : 343-393.

Source : MNHN, Paris

ORENSANZ, J.M., 1990. — The eunicemorph Polychaeta from Antarctic and Subantarctic Seas, with addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia and the Southern Indian Ocean. *Antarct. Res. Ser.*, **52** : 1-183.

PERKINS, T.H., 1979. — Lumbrineridae, Arabellidae, and Dorvilleidae (Polychaeta), principally from Florida, with descriptions of six new species. *Proc. biol. Soc. Wash.*, **92** : 415-465.

PETTIBONE, M.H., 1963. — Marine polychaete worms of the New England region. 1. Aphroditidae through Trochochaetidae. *Bull. U.S. Natl. Mus.*, **227** : 1-356.

RAMOS, J.M., 1976. — Lumbrineridae (Polychètes Errantes) de Méditerranée. *Ann. Inst. océanogr.*, **56** : 103-137.

SALEN-PICARD, C., 1982. — *Contribution à l'étude dynamique de peuplements marins de substrats meubles : les peuplements macrobenthiques circalittoraux soumis à l'envasement dans la région Provencale.* Thèse Doct. Etat Sciences Naturelles, Université d'Aix-Marseille II, 265 pp.

UEBELACKER, J.M., 1984. — Family Lumbrineridae. *In*: J.M. UEBELACKER & P.F.G. JOHNSON (eds.), *Taxonomic guide to polychaetes of the northern Gulf of Mexico*. Barry A. VITTOR & Associates, Inc., Mobile, Alabama, **41** : 1-45.

VAMVAKAS, C., 1970. — Peuplements benthiques des substrats meubles du sud de la Mer Égée. *Tethys*, **2** : 89-130.

VOULTSIADOU-KOUKOURA, E., KOUKOURAS, A. & A. ELEFTHERIOU, 1987. — Macrofauna associated with the sponge *Verongia aerophola* in the North Aegean Sea. *Estuar. Coast. Shelf Sci.*, **24** : 265-278.

Source : MNHN, Paris

# Autolytinae (Polychaeta, Syllidae) from Cuba and north American Atlantic Ocean

*Guillermo SAN MARTIN*

Laboratorio de Invertebrados Marinos, Unidad de Zoología
Departamento de Biología, Facultad de Ciencias
Universidad Autónoma de Madrid
Canto Blanco, E-28049, Madrid, Spain

ABSTRACT

This paper treats nine species of the subfamily Autolytinae (Polychaeta, Syllidae), principally from Cuba, and also from North Carolina and Massachusetts. One new species is described, *Autolytus juventudensis*. Four species: *Autolytus convolutus* Cognetti, 1953; *A. tamanus* Imajima, 1966; *A. quindecimdentatus* Langerhans, 1884; and *A. dentalius* Imajima, 1966, are newly reported for Cuba; all these species except the last are also new to the Caribbean and Gulf of Mexico. *Autolytus inermis* Saint-Joseph, 1887 is new to North Carolina.

RÉSUMÉ

**Autolytinae (Polychaeta, Syllidae) de Cuba et des côtes américaines de l'Atlantique Nord**

Ce travail présente une étude de neuf espèces d'Autolytinae (Polychaeta, Syllidae) de Cuba, de Caroline du Nord et du Massachusetts (Etats-Unis). On décrit une nouvelle espèce, *Autolytus juventudensis*. Quatre espèces : *A. convolutus* Cognetti, 1953 ; *A. tamanus* Imajima, 1966 ; *A. quindecimdentatus* Langerhans, 1884 et *A. dentalius* Imajima, 1966, sont nouvelles pour Cuba. Ces espèces, à l'exception de la dernière, sont aussi nouvelles pour les Caraïbes et le golfe du Mexique. *Autolytus inermis* Saint-Joseph, 1887 est nouvelle pour la Caroline du Nord.

## INTRODUCTION

This is the seventh paper treating syllids collected in Cuba during the "Primera Expedición Cubano-Española a la Isla de la Juventud (Isle of Pines) y Archipiélago de los Canarreos", and elsewhere in neighbouring areas (SAN MARTIN, 1990, 1991 a, b, c, d, 1992). The material from North Carolina and Massachusetts was loaned by the Zoological Museum, University of Copenhagen (ZMUC), and were mostly collected by Dr. Mary E. Petersen during 1961-1963 and 1984.

---

SAN MARTIN, G., 1994. — Autolytinae (Polychaeta: Syllidae) from Cuba and North American Atlantic Ocean. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 269-277. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## MATERIAL AND METHODS

Types and other specimens are deposited in the Museo Nacional de Ciencias Naturales de Madrid (MNCNM), Spain, the Zoological Museum, University of Copenhagen (ZMUC), and the author's collection.

Measurements refer to the holotype or the largest specimen studied; width was measured at the proventricular level, without cirri, parapodia or setae. Microscope mounts were made in glycerine jelly of some of the complete specimens and some parapodia. Drawings and measurements were made using a compound microscope with differencial interference contrast optics (Nomarsky). Drawings were made using a camera-lucida drawing tube.

A more extensive introduction and additional information about methods and materials have been given in SAN MARTIN *et al.*, (1986).

PERKINS & SAVAGE (1975), UEBELACKER (1984), IBARZABAL (1986, 1988), DAY (1973), and GARDINER (1976) were used for determination of the new geographical records.

## SYSTEMATICS

Family Syllidae Grube, 1850

Subfamily Autolytinae Rioja, 1925

Genus ***Myrianida*** Milne-Edwards, 1845

### ***Myrianida*** sp.

MATERIAL EXAMINED. — Cuba: Between Punta del Este, Isle of Pines, and Cayo Matías, Archipiélago de los Canarreos, from algae at 18 m depth, two incomplete specimens, from *Halimeda* sp. in *Thalassia testudinum* beds at 3 m depth, one incomplete specimen.

REMARKS. — The three anterior fragments have a trepan with 50-60 triangular, equal teeth and a small proventriculus, occupying two segments, with about 10 rows of large muscle cells. *Myrianida pinnigera* (Montagu, 1808) from the Mediterranean Sea has a similar trepan, but the proventriculus is longer and with more muscle cell rows. Other known species of *Myrianida* have fewer teeth in the trepan, longer proventriculus, and with more rows of muscle cells than these specimens from Cuba.

DISTRIBUTION. — Cuba.

Genus ***Proceraea*** Ehlers, 1864

### ***Proceraea*** sp.

MATERIAL EXAMINED. — Cuba: Punta Pedernales, Isle of Pines in living coral from 1.5 m depth, two specimens. Canal de los Vapores, Cayo Bocas de Alonso, Archipiélago de los Canarreos in sponges on *Rhizophora mangle* roots at 0.5 m depth, four specimens. Cayo Matías, Archipiélago de los Canarreos from *Halimeda* sp., seven specimens. North Carolina, Bogue Sound in sand and shells, 2-4 m depth, two specimens (ZMUC).

REMARKS. — All species of this genus are very similar. The colour pattern is an important differential character; since all the examined specimens have lost their colouration, it was not possible to identify them.

DISTRIBUTION. — Cuba and North Carolina.

Genus ***Autolytus*** Grube, 1850

### ***Autolytus convolutus*** Cognetti, 1953

*Autolytus convolutus* Cognetti, 1953: 323, pl. I, fig. 1-2 (type-locality: Gulf of Naples). — COGNETTI, 1957: 71, fig. 15. — BEN-ELIAHU, 1972: 217, fig. 14 a-d; 1977: 85, fig. 12. — SAN MARTIN, 1984: 413, pl. 111.

Source : MNHN, Paris

***Autolytus (Regulatus) convolutus*** — IMAJIMA, 1966: 47, fig. 12 a-h.

MATERIAL EXAMINED. — Cuba: Canal de los Vapores, Cayo Bocas de Alonso, Archipiélago de los Canarreos from hydroids on *Rhizophora mangle* roots at 0.5 m depth, four specimens. Cayo Matías, Archipiélago de los Canarreos from *Turbinaria turbinata* at 3 m depth, one specimen and from *Halimeda* sp. at 3 m depth, seven specimens.

REMARKS. — Three specimens have 16 pharyngeal teeth on the trepan instead of nine as usually reported for this species; however, in the original description COGNETTI (1953) described several specimens having 15- 16 teeth. The remaining characters agree with the diagnosis of this species.

DISTRIBUTION. — Mediterranean Sea, Suez Canal, Japan, Cuba.

***Autolytus alexandri*** Malmgren, 1867

*Autolytus alexandri* Malmgren, 1867: 37, pl. VII, fig. 39 (type-locality: Davis Strait, Greenland). — PETTIBONE, 1963: 147, fig. 37 f, g.

*Autolytus longeferiens* Saint-Joseph, 1887. — FAUVEL, 1923: 319, figs 122 h-k. — GIDHOLM, 1967, figs. 2 C, 7 G, 13 C, 27.

Non *Autolytus alexandri* — HARTMAN, 1945: 17, pl. 2, fig. 11.

MATERIAL EXAMINED. — Massachusetts, off Nobska Light, Vineyard Sound in sand, shells, stones and masses of *Amaroucium pellucidum* at 6-7.5 m depth, two specimens (ZMUC).

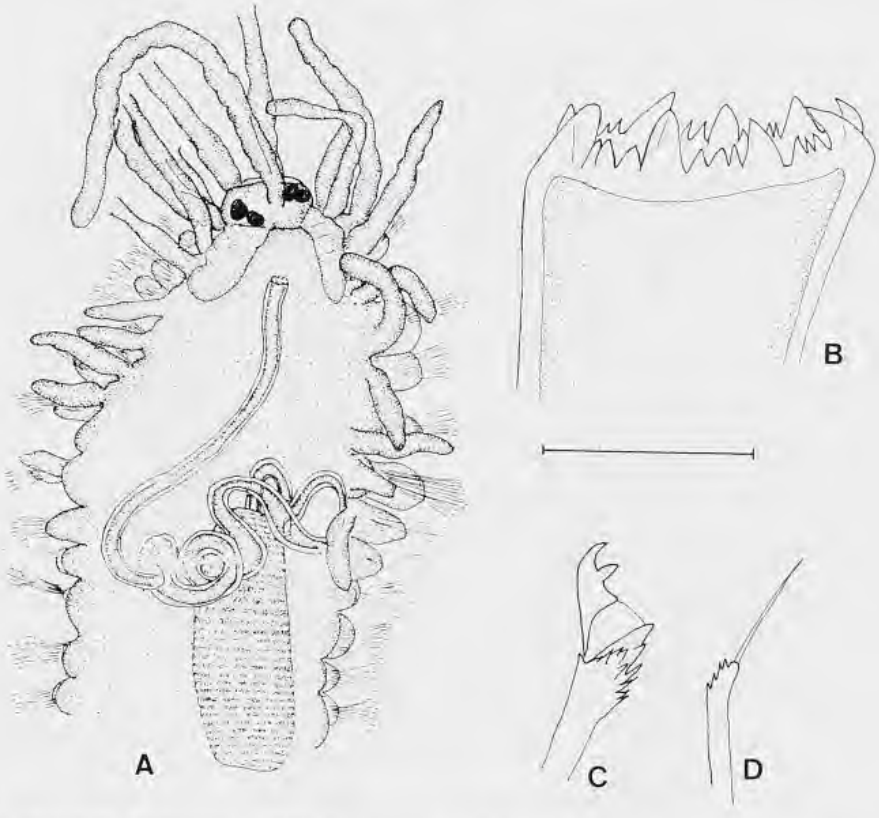



FIG. 1. — *Autolytus alexandri* Malmgren, 1867: A, anterior end, dorsal view. B, trepan. C, compound seta. D, dorsal simple seta. Scale. A: 0.2 mm. B, C, D: 20 µm.

Source : MNHN, Paris

DESCRIPTION. — Body broad, especially anteriorly, dark orange, 0.28 mm wide, 2.5 mm long for 40 setigers (Fig. 1). Prostomium small, with four large eyes and close on each side. One specimen also had two additional small anterior eyespots. Palps small. Median antenna long, cylindrical, originating from the middle of prostomium; lateral antennae damaged on both specimens. Tentacular cirri broken on both specimens. Nuchal epaulettes reaching setiger 2. Dorsal cirri of first setiger relatively long, similar in length to body width; remaining dorsal cirri shorter than body width; cirrophores shorter than parapodial lobes. Parapodial lobes rounded. Parapodia each with about 5-9 compound setae; blades short, strongly bidentate, with both teeth similar, hooked. Solitary dorsal simple seta from proventricular setigers. Pharynx very long, with numerous sinuations. Trepan with nine large teeth separated by two-three smaller teeth. Proventriculus long through about four-six segments and with about 40 rows of muscle cells.

REMARKS. — GIDHOLM (1967) suggested that *A. alexandri* from North America and the Arctic Ocean are identical to *A. longeferiens* from northern Europe. Since the Massachusetts specimens examined agree with descriptions of both species, these two species appear to be synonymous.

DISTRIBUTION. — Arctic, Iceland, North American coasts from Labrador to Massachusetts, and from the Bering Sea to Washington, European Atlantic coasts from Skagerrak to France.

### *Autolytus tamanus* Imajima, 1966

*Autolytus (Autolytus) tamanus* Imajima, 1966: 46, text-fig. 11 e-k (type-locality: Karasu-jima, near Tamano, Japan).

MATERIAL EXAMINED. — Cuba: Punta Pedernales, Isle of Pines in living coral at 1.5 m depth, three specimens.

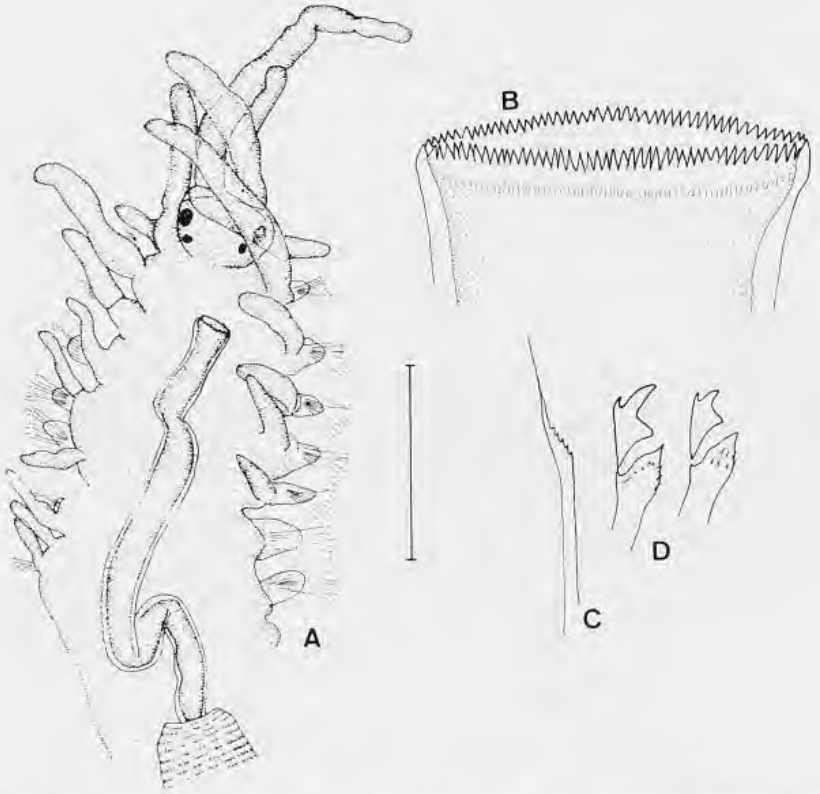



FIG. 2. — *Autolytus tamanus* Imajima, 1966: A, anterior end, dorsal view. B, trepan. C, dorsal simple seta. D, compound setae. Scale. A: 0.2 mm. B: 40 µm. C, D: 20 µm.

Source : MNHN, Paris

DESCRIPTION. — Body small, without colour markings, 0.48 mm wide, 4 mm long for 38 setigers (stolons not included). Prostomium rounded with four large eyes in open trapezoidal arrangement (Fig. 2). Antennae, tentacular cirri and dorsal cirri of first setiger longer than body width; remaining dorsal cirri more or less conical, alternating as long and short cirri. Nuchal epaulettes not seen. Parapodia rounded, shorter than dorsal cirri, each with about 15 setae which are provided with long proximal tooth and small distal tooth. Solitary dorsal simple setae bayonet-shaped on posterior segments. Pharynx long, with one sinuation extending from setiger 2 to setiger 9; trepan with about 90 small teeth. Proventriculus long through about 5 segments provided with about 30-40 rows of muscle cells. Anal cirri conical, much longer than dorsal cirri. One specimen with three attached terminal sexual stolons.

DISTRIBUTION. — Southern Japan, Cuba.

### *Autolytus juventudensis* sp. nov.

MATERIAL EXAMINED. — Cuba: off Punta del Francés, Isle of Pines in dead coral at 1 m depth; holotype and two paratypes (MNCNM). Punta Pedernales, Isle of Pines in living coral at 1.5 m depth, two juvenile specimens.

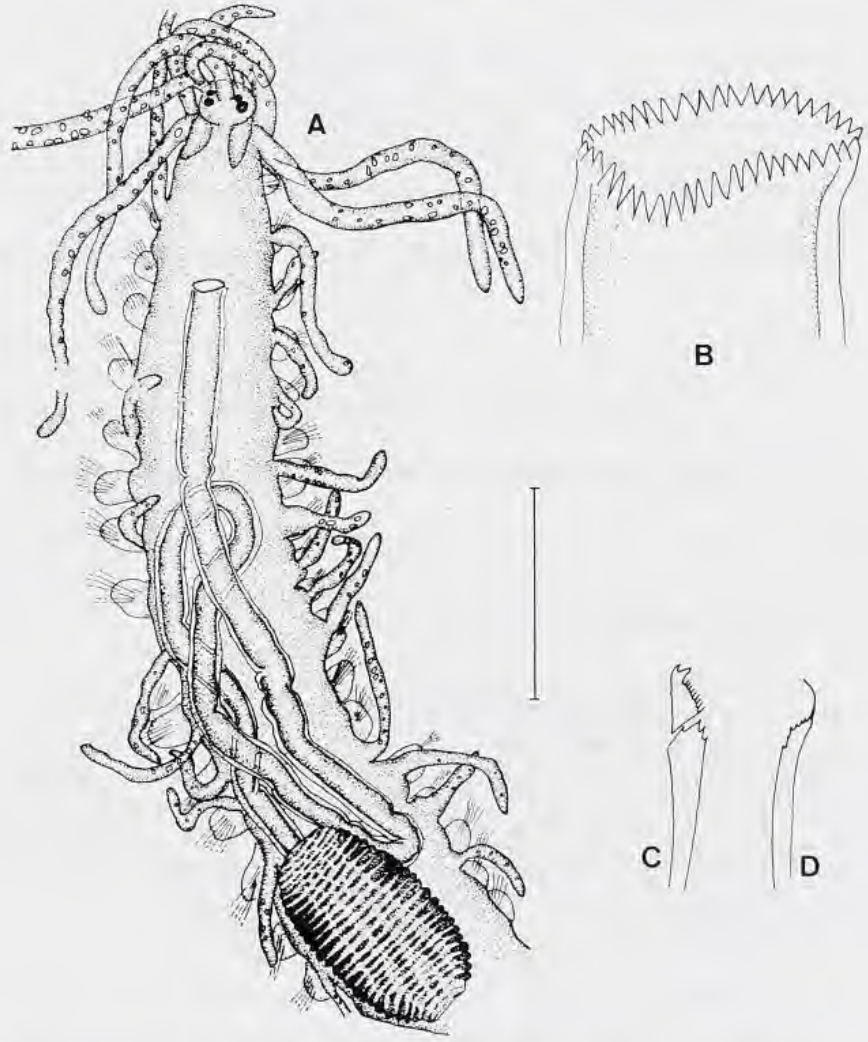



FIG. 3. — *Autolytus juventudensis* n. sp. Holotype: A, anterior end, dorsal view. B, trepan. C, compound seta. D, dorsal simple seta. Scale. A: 0.2 mm. B: 40 µm. C, D: 20 µm.

Source : MNHN, Paris

DESCRIPTION. — Body long, slender, holotype 0.28 mm wide, 4.6 mm long for 60 setigers (Fig. 3). Prostomium small, rounded, with two pairs of large eyes, palps small, fused, not visible dorsally; antennae long, extending to at least setiger 8. Nuchal epaulettes small, oval, reaching setiger 1. Dorsal tentacular cirri shorter than antennae; ventral tentacular cirri about half the length of the dorsal cirri. Dorsal cirri of setiger 1 long, shorter than dorsal tentacular cirri; dorsal cirri of setiger 2 shorter than dorsal cirri of setiger 1; remaining dorsal cirri proportionally long, alternating irregularly long, similar in length to body width, and shorter. Antennae, tentacular and dorsal cirri provided with small, rounded, hyaline inclusions. Pygidium small, with two long anal cirri. Parapodia rounded, each with about 7-8 compound setae with short blades and provided with a proximal a tooth somewhat larger than distal tooth. Solitary dorsal simple seta bayonet-shaped, slender, from about setiger 8. Pharynx very long with two long coils, trepan in setiger 3 with about 43 small, equal teeth. Proventriculus from setiger 14 to setiger 18 with about 25 rows of muscle cells.

REMARKS. — *Autolytus juventudensis* is characterized by having a slender body with relatively long dorsal cirri, a long and coiled pharynx and a trepan of more than 40 equal teeth. This species is similar to *A. magnus* Berkeley, 1923 from Alaska and Japan, but the blades of the compound setae are very different (see IMAJIMA & HARTMAN, 1964). The two teeth of the blades are similar and hooked in *A. magnus*, in contrast to the typical shape for the genus in *A. juventudensis*. Compound setae of *A. irregularis* Imajima & Hartman, 1964 from Japan are very similar to those of *A. juventudensis*; however, the former has a trepan with only 21-27 teeth and the nuchal epaulettes extend through five segments, and the latter has more than 40 teeth in the trepan and the nuchal epaulettes are shorter.

The two juvenile specimens have a proportionally shorter pharynx with fewer coils and about 33 teeth in the trepan; proventriculus shorter and extending through about four segments and provided with about 32 rows of muscle cells. The juvenile specimens are very similar to *A. prolifer*; however, the dorsal cirri are proportionally longer and are provided with refringent granules which are absent in *A. prolifer*. Adults of *A. juventudensis* differ from *A. prolifer* in the number of pharyngeal teeth and in the length of the pharynx and proventriculus.

ETYMOLOGY. — The specific name comes from Isla de la Juventud = Isle of Pines), the type locality of this species.

DISTRIBUTION. — Cuba.

### *Autolytus inermis* Saint-Joseph, 1887

*Autolytus inermis* Saint-Joseph, 1887, p. 237, fig. 117 (type-locality: Dinard, France). — GIDHOLM, 1967: 193, figs 7 D-E, 22.

*Autolytus (Autolytides) inermis* — FAUVEL, 1923: 322, figs 123 h-k.

MATERIAL EXAMINED. — North Carolina: Bogue Sound from sand and shells at 2-4 m depth, two specimens (ZMUC). Core Sound, Cowpen Island from empty shells, one specimen (ZMUC).

DESCRIPTION. — Body proportionally short and broad, yellowish, without colour pattern, 0.32 wide, 4 mm long for 71 setigers (Fig. 4). Prostomium rounded with two pairs of large eyes in open trapezoidal arrangement; antennae relatively short and thick, cylindrical. Palps fused, not visible dorsally. Tentacular cirri relatively short, similar to antennae. Nuchal epaulettes long extending to setiger 4. Segments well marked dorsally. Dorsal cirri shorter or equal in length to half of body width, with long cirrophores, alternating irregularly long and short dorsal cirri. Parapodia each with 5-6 similar compound setae with short blades, proximal tooth somewhat larger than distal tooth. Solitary dorsal simple setae bayonet-shaped on posterior segments. Pharynx from setiger 2 to setiger 11 with a terminal coil. Trepan indistinct with about 26 very small, subequal teeth. Proventriculus small extending through about 6 segments with 12-14 rows of thick muscle cells.

REMARKS. — The northern European and French specimens described by GIDHOLM (1967) have proportionally longer antennae and anterior dorsal cirri as well as a longer pharynx. However, I do not think that these small differences justify erecting a new taxon for these specimens from North Carolina.

DISTRIBUTION. — Northern-European Atlantic coasts, North Carolina.

Source : MNHN, Paris

### *Autolytus quindecimdentatus* Langerhans, 1884

*Autolytus quindecimdentatus* Langerhans, 1884: 249, fig. 3 a-b (type-locality: Madeira, Portugal). — GIDHOLM, 1967: 197, figs 7 f, 12, 23 a. — CAMPOY, 1982: 241. — SAN MARTIN, 1984: 417, pl. 113.

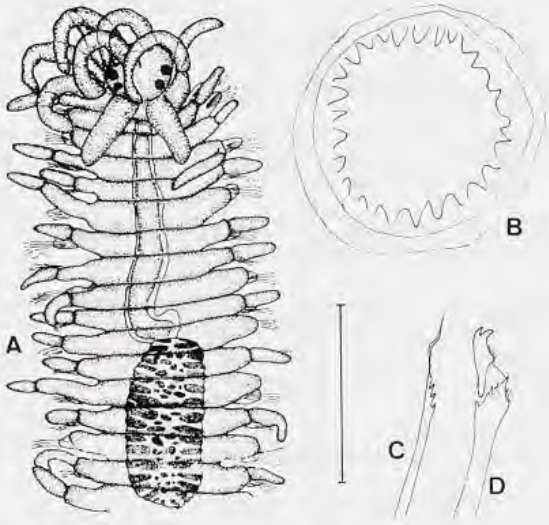



FIG. 4. — *Autolytus inermis* de Saint-Joseph, 1887: A, anterior end, dorsal view. B, mouth of the pharynx. C, dorsal simple seta. D, compound seta. Scale. A: 0.2 mm. B, C, D: 20 µm.

MATERIAL EXAMINED. — Cuba: Off Cayo Matías from *Turbinaria turbinata* at 3 m depth, nine specimens, from *Stypopodium zonale* at 3 m depth, one specimen. Between Punta del Este and Cayo Matías from algae at 18 m depth, one specimen and from *Halimeda* sp. in *Thalassia testudinum* beds at 3 m depth, two specimens. Off Punta del Francés, Isle of Pines from algae at 4 m depth, four specimens. Off Cayo Matías from *Halimeda* sp. at 3 m depth, five specimens.

DISTRIBUTION. — Mediterranean Sea, Atlantic European and African coasts, from Scandinavia to Canary Islands, Red Sea, Cuba.

### *Autolytus dentalius* Imajima, 1966

*Autolytus (Autolytus) dentalius* Imajima, 1966: 36, fig. 7 i-l (type-locality: Senda-Zaki, in Uraga Strait, Japan). — DAY, 1973: 35. — GARDINER, 1976: 127, fig. 10 a-d. — UEBELACKER, 1984: 30-12, fig. 30-4.

MATERIAL EXAMINED. — Massachusetts, off Nobska Light, Vineyard Sound from sand, shells, stones, and masses of *Amaroucium pellucidum* at 6-7.5 m depth, one specimen (ZMUC). North Carolina, Bogue Sound from shells and sand at 2-4 m depth, 73 specimens (ZMUC). Cuba: Off Punta del Francés, Isle of Pines from in dead coral at 1 m depth, four specimens. Off Cayo Matías, Archipiélago de los Canarreos from *Halimeda* sp. at 3 m depth, one specimen. Off Punta del Francés from algae at 4 m depth, one specimen.

DISTRIBUTION. — Japan, Massachusetts, North Carolina, Gulf of Mexico, Cuba.

Source : MNHN, Paris

## ACKNOWLEDGEMENTS

I wish to express my gratitude to all members of the Cuban-Spanish Expedition, especially to the Cuban researchers from the Centro de Investigaciones Marinas de la Universidad de La Habana. Dr. Mary E. PETERSEN, Zoological Museum of the University of Copenhagen, Denmark, loaned the material from Massachusetts and North Carolina, offered useful advice to me, and revised the manuscript, as well as two anonymous referees.

## REFERENCES

BEN-ELIAHU, M. N., 1972. — Polychaeta Errantia from the Suez Canal. *Isr. J. Zool.*, **21** : 189-237.

BEN-ELIAHU, M. N., 1977. — Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coasts of Israel and in the Gulf of Elat: Exogoninae and Autolytinae (Polychaeta Errantia: Syllidae). *Isr. J. Zool.*, **26** : 59-99.

BERKELEY, E., 1923. — Polychaetous Annelids from the Nanaimo District. Part I. Syllidae to Sigalionidae. *Contribs. Canad. Biol.*, **1** : 203-218.

CAMPOY, A., 1982. — *Fauna de España. Fauna de Anélidos Poliquetos de la Península Ibérica*. EUNSA (Ediciones de la Universidad de Navarra, S. A.), 781 pp.

COGNETTI, G., 1953. — Osservazioni sulla biologia riproduttiva di una nuova spece di *Autolytus* del Golfo di Napoli. *Arch. Zool. It.*, **38** : 323-332.

COGNETTI, G., 1957. — I sillidi del Golfo di Napoli. *Pubbl. Staz. Zool. Napoli*, **30** : 1-100.

DAY, J. H., 1973. — New Polychaeta from Beaufort with a key to all species recorded from North Carolina. *NOAA Tech. Rep. NMFS Circ.*, **375** : 1- 140.

FAUVEL, P., 1923. — Polychètes Errantes. *Faune Fr.*, **5** : 1- 488.

GARDINER, S. L., 1976. — Errant polychaete annelids from North Carolina. *J. Elisha Mitchell Sci. Soc.*, **91** : 78-220.

GIDHOLM, L., 1967. — A revision of Autolytinae (Syllidae, Polychaeta) with special reference to Scandianvian species, and with notes on external and internal morphology, reproduction and ecology. *Ark. Zool.*, **19** : 157-213.

HARTMAN, O., 1945. — The marine annelids of North Carolina. *Duke Univ. Mar. Sta. Bull.*, **2** : 1-54.

IBARZABAL, D., 1986. — Lista de especies de poliquetos bentónicos cubanos. *Rep. Invest. Inst. Oceanol.*, **45** : 1-17.

IBARZABAL, D., 1988. — Poliquetos de Punta del Este, Isla de la Juventud. II. Familias Phyllodocidae, Hesionidae y Syllidae. *Poeyana*, **359** : 1-10.

IMAJIMA, M., 1966. — The Syllidae (polychaetous annelids) from Japan (II), Autolytinae. *Publ. Seto Mar. Biol. Lab.*, **14** : 27-83.

IMAJIMA, M. & HARTMAN, O., 1964. — The polychaetous annelids of Japan. *Allan Hancock Found. Occ. paper*, **26** : 1-452.

LANGERHANS, P., 1884. — Die Würmfauna von Madeira. IV. *Zeitschr. Wiss. Zool.*, **40** : 247-285.

MALMGREN, A. J. 1861. — Annulata Polychaeta. Spetsberglae, Groenlandiae, Islandiae et Scandinaviae Hactemus Cognita. *Forh. Oefv. K. Vetensk. Akad. Stockholm*, **24** : 1-125.

MONTAGU, G. 1808. — New and rare animals found on the South Coast of Devonshire. *Trans. Linn. Soc. London*, **9** : 108- 111.

PERKINS, T. H. & SAVAGE, T., 1975. — A bibliography and checklist of polychaetous annelids of Florida, the Gulf of Mexico, and the Caribbean region. *Florida Mar. Res. Publ.*, **14** : 1-62.

PETTIBONE, M. H., 1963. — Marine Polychaete worms of the New England region. 1. Aphroditidae through Trochochaetidae. *Bull. U. S. Nat. Mus.*, **227** : 1- 356.

SAINT-JOSEPH, Baron de, 1887. — Les annélides polychètes des côtes de Dinard. *Ann. Sci. Natur. Zool.*, sér. 7, **1** : 127-270.

Source : MNHN, Paris

SAN MARTIN, G., 1984. — *Estudio biogeográfico, faunístico y sistemático de los Poliquetos de la Familia Sílidos (Polychaeta: Syllidae) en Baleares*. Tesis Doctoral. Ediciones de la Universid Complutense de Madrid, **186** : 529 pp.

SAN MARTIN, G., 1990. — Eusyllinae (Syllidae, Polychaeta) from Cuba and the Gulf of Mexico. *Bull. Mar. Sci.*, **46** : 590-619.

SAN MARTIN, G., 1991 a. — *Sphaerosyllis* and *Parapionosyllis* (Exogoninae, Syllidae, Polychaeta) from Cuba, Florida and the Gulf of Mexico. *Ophelia* Suppl., **5** : 231-238.

SAN MARTIN, G., 1991 b. — Syllinae (Polychaeta: Syllidae) from Cuba and the Gulf of Mexico. *Bull. Mar. Sci.*, **48** (2) : 227-235.

SAN MARTIN, G., 1991 c. — A new species of *Pionosyllis* Malmgren, 1887 (Polychaeta: Syllidae: Eusyllinae), from Cuba. *Graellsia*, **47** : 17- 20.

SAN MARTIN, G., 1991 d. — *Grubeosyllis* and *Exogone* (Exogoninae, Syllidae, Polychaeta) from Cuba, Puerto Rico, Florida and the Gulf of Mexico, with a revision of *Exogone*. *Bull. Mar. Sci.*, **49** : 715-740.

SAN MARTIN, G., 1992. — *Syllis* Savigny in Lamarck, 1818 (Polychaeta: Syllidae: Syllinae) from Cuba, the Gulf of Mexico, Florida and North Carolina, with a revision of several species described by Verrill. *Bull. Mar. Sci.*, **51** : 167-196.

SAN MARTIN, G., AGUIRRE, O. & BARATECH, L., 1986. — Anélidos Poliquetos procedentes de la I Expedición Cubano-Española a la Isla de la Juventud y Archipiélago de los Canarreos. I. Familias Polynoidae, Sigalionidae, Pholoididae y Pisionidae. *Rev. Inv. Mar.*, **7** (1) : 3-16.

UEBELACKER, J. M., 1984. — Family Syllidae Grube, 1850. *In*: J.M. UEBELACKER & P. G. JOHNSON (eds.), *Taxonomic guide to the polychaetes of the northern Gulf of Mexico*. Barry A. VITTOR & Associates, Mobile, **30** : 1-151.

Source : MNHN, Paris

Source : MNHN, Paris

# New arctic species of *Scolelepis* (Polychaeta, Spionidae)

*Andrew V. SIKORSKI*

Zoological Museum of the Moscow Lomonosov State University
Herzen Street 6, K-9, Moscow 103009, Russia.

ABSTRACT

Three new species of *Scolelepis* were present in the Russian collections from the Arctic Ocean and the border areas *S. matsugae*, *S. burkovskii* and *S. korsuni*. All these are from the Barents Sea. *S. korsuni* is known also from the nothern part of the North Sea, and *S. matsugae* from the Kara Sea and Franz-Josef Land. There are no another species of *Scolelepis* in the Russian arctic zoological collections. The diagnostic characters for *S. korsuni* are: presence of superior flag-like process in middle dorsal lamellae, absence of setae in first notopodiae, shape of hooks and their number; for *S. matsugae*: shape of prostomium, shape of hooks, setiger of hooks starting and pattern of branchiae decreasing. *S. burkovskii* separated by complex of characters. Five species with *S. squamatus* (O.F.Müller, 1806) and *S. foliosus* (Audouin & Milne Edwards, 1833) are now known from the Arctic Ocean and the border areas.

RÉSUMÉ

**Nouvelles espèces arctiques du genre *Scolelepis* (Polychètes, Spionidae)**

Trois nouvelles espèces de *Scolelepis* ont été trouvées dans les collections russes de l'océan Arctique et des mers polaires : *S. matsugae*, *S. burkovskii* et *S. korsuni*. Ces trois espèces proviennent de la mer de Barents. *S. korsuni* est aussi présente dans la partie nord de la mer du Nord, et *S. matsugae* dans la mer de Kara et près de la Terre François-Joseph. Les caractères distinctifs de *S. korsuni* sont les suivants : la présence d'expansion en forme de drapeau au milieu de la lamelle dorsale, l'absence de soies dans les premiers notopodes, la forme et le nombre des crochets ; ceux de *S. matsugae* sont : la forme du prostomium et des crochets, le niveau d'apparition du premier sitigère avec des crochets et la forme de la branchie. *S. burkovskii* a été séparée des autres espèces par plusieurs caractères. Cinq espèces, y compris *S. squamatus* (O.F. Müller, 1806) et *S. foliosus* (Audouin & Milne Edwards, 1833), sont maintenant connues dans l'océan Arctique.

## INTRODUCTION

Only two species of *Scolelepis* de Blainville, 1828, *S. squamatus* (O.F. Müller, 1806) and *S. foliosus* (Audouin & Milne Edwards, 1833), are known from the Arctic Ocean and the border areas. The former has been recorded off Iceland (WESENBERG-LUND, 1951) and from the Norwegian Sea (HARTMANN-SCHRÖDER, 1971);

SIKORSKI, A.V., 1994. — New arctic species of *Scolelepis* (Polychaeta, Spionidae). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 279-286. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

the latter species is known from the Norwegian coast to Finmark (SARS, 1851, 1873). An examination of all Russian collections from the area (about 2,500 samples) revealed an additional three new species from the Barents Sea (with the Franz-Josef Land) and the Kara Sea.

## MATERIAL

Specimens described in this paper are deposited in Zoological Museum, Moscow Lomonosov State University (ZMUM), Zoological Institution of St. Petersburg (ZIN), Zoological Museum, University of Copenhagen (ZMUC), Muséum National d'Histoire Naturelle of Paris (MNHN) and the reference collection of Akvaplan-niva (AKV), consulting firm, Tromsø, Norway.

## SYSTEMATICS

### *Scolelepis* de Blainville, 1828

DIAGNOSIS. — Prostomium anteriorly pointed or bluntly rounded, extending posteriorly as a narrow caruncle. Occipital crest generally well developed, sometimes forming occipital tentacle; 0-2 pairs of eyes. Peristomium generally not fused with setiger 1, lateral wings variously developed. Neuropodial hooded hooks present, notopodial hooded hooks present or absent; secondary hoods sometimes present. Sabre setae absent. Flattened branchiae from setiger 2 on anterior half of body, sometimes continuing to posterior end. Anterior branchiae completely or mostly fused with dorsal lamellae. Dorsal nuchal organ (according to SÖDERSTRÖM, 1920) restricted to small areas on either side of posterior caruncle. Anus terminal or dorsal. Pygidium with ventral cushion (incised or entire), oval or multilobed membrane. Dark pigmentation resistant to alcohol, occurs primarily on the prostomium and pygidium.

I agree with the point supported by BLAKE & KUDENOV (1978) and MACIOLEK (1987) that many exceptions occur with the set of characters making the separation of the genera *Scolelepis* de Blainville, 1828 and *Nerinides* Mesnil, 1896 unfeasible at this time.

Separation of subgenus *Parascolelepis* proposed by MACIOLEK (1987) seems interesting, but I am not sure if it is possible in *Scolelepis*-genus to use the shape of hooded hooks for separating taxa above species. We can see gradations in the genus between the falciger-like type of hooks with 0-3 short apical teeth for subgenus *Scolelepis* and sharp-fanged, multidentate hooks for subgenus *Parascolelepis*. Moreover, there are many species in the genus showing both individual and size variation of the shape of hooded hooks. I think that more useful character might be the presence of a sheath at the base of the palps, but I do not have complete information for all species. I do not separate these two subgenera herein.

### *Scolelepis korsuni* sp.nov.

? *Nerinides tridentata* — HANNERZ, 1956: 9-11, Fig.1(a-c). —KIRKEGAARD, 1969: 79, Fig. 42.

MATERIAL EXAMINED. — North Sea. coll. AKV for Elf Aquitaine: stn 4-1 (LILLE FRIGG II), 59°57'42"N, 2°23'44"E, 108 m, 11.V.1992: holotype (ZMUC). Forty samples (LILLE FRIGG II), from 59°56' to 60°01'30"N, from 2°20' to 2°25'45"E, 95-111 m, 7-11.V.1992: 78 paratypes (ZMUM Pl 1/883-6/888, 8/890-13/895, 15/897-24/906, 25/910-45/930 ; ZIN 1/48517, 2/48518 - two specimens; five specimens in AKV; one specimen in MNHN). Ten samples (NØ FRIGG), from 59°57'40" to 60°01'30"N, from 2°12' to 2°23'30"E, 95-110 m, 13-14 and 17-18.V.1992: 10 paratypes (ZMUM Pl 47/932-51/936; five specimens in AKV). five samples (HEIMDAL), from 59°34' to 59°36'N, from 2°11'40" to 2°14'15"E, 114-116 m, 15-17.V.1992: five paratypes (ZMUM Pl 7/889, 14/896, 46/931; two specimens in AKV). Barents Sea. R/V "Tunets": stn 105.20, 73°01'N, 22°00'E, 440-450 m, silt, 1.16°C, 4.VII.1978: one paratype (ZMUM Pl 52/824).

DESCRIPTION. — Holotype complete, 1.2 mm wide and 13.2 mm long, 46 setigers, without palps. Fig. 1a-h.

The smallest specimen (ZMUM Pl 899), 0.6 mm wide and 6.6 mm long for 34 setigers. The longest complete specimens (ZMUM Pl 882, 886, 901), 1-1.2 mm wide and 11-13 mm long for 40-46 setigers. The longest incomplete specimen (ZMUM Pl 900), 1.6 mm wide and 21 mm long for 51 setigers. The largest

Source : MNHN, Paris

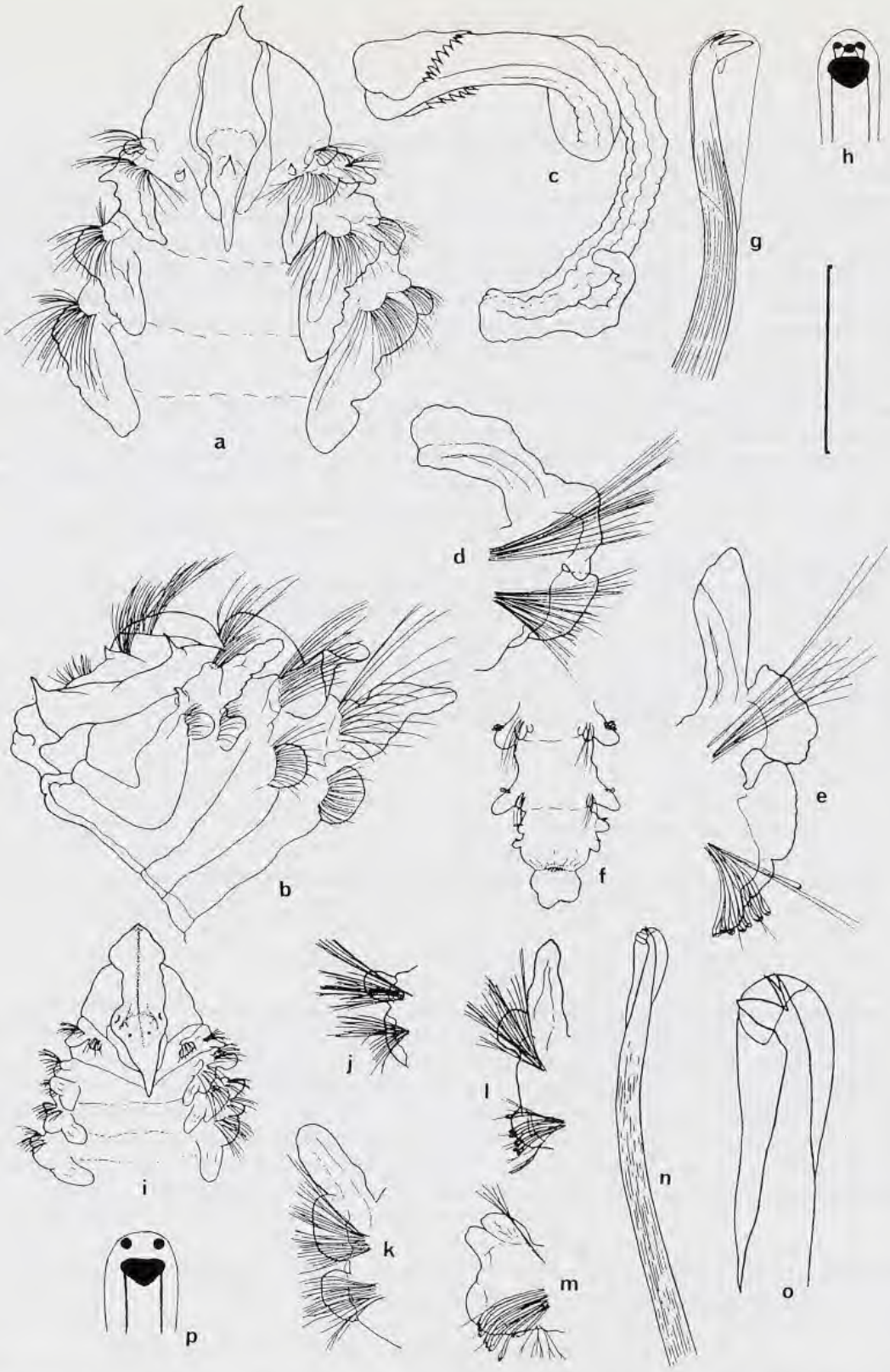



FIG. 1. — *Scolelepis korsuni* sp. nov.: a, anterior end through first 4 setigers, in dorsal view (palps missing). - b, same anterior end, in lateral view. - c, palp. - d, parapodium of setiger 8. - e, parapodium of setiger 19. - f, pygidium. - g, a hooded hook of parapodium 21 (in lateral view). - h, distal end of same seta (in frontal view - scheme). — *Scolelepis burkovskii* sp. nov. : i, anterior end through first 4 setigers, in dorsal view (palps missing). - j, first parapodium. - k, seventh parapodium. - l, parapodium 17. - m, a posterior, or second last, parapodium. - n, a hooded hook from parapodium 18, in frontal-lateral view. - o, distal end of same seta. - p, distal end of same seta (in frontal view - scheme). Scale: a-b, 1 mm; c, f, 1.4 mm; d, 0.6 mm; e, 0.4 mm; g, 0.06 mm; i, 0.56 mm; j-m, 0.28 mm; n, 0.044 mm; o, 0.017 mm.

Source : MNHN, Paris

incomplete specimen (ZMUM Pl 889), 2.1 mm wide and 11 mm long for 26 setigers.

Prostomium spindle-shaped, anteriorly projecting, elongate (Fig. 1-a) narrowing posteriorly into pointed caruncle reaching posterior margin of setiger 2 (visible only if stained with methyl green). Eyes usually absent; one specimen (ZMUM Pl 932) had two pairs small rounded eyespots of nearly equal size arranged in transverse line slightly curved toward anterior end. Occipital crest more or less pronounced. Occipital tentacle pointed, erected and oriented usually anteriorly. Grooves between prostomium and peristomium narrow. Palps long sometimes reaching middle of body, with cogged basal sheath (Fig. 1-c). Lateral wings of peristomium are low. There are small folds surrounding the place of palp's attachment. Pharynx often eversed. The posterior ventral border of setiger 1 is clearly visible oriented toward the mouth (Fig. 1-b).

Branchiae from setiger 2, completely fused to longer notopodial lamellae (Fig. 1-d). From setiger 14-19 notopodial lamellae deeply notched at level of branchial bases (Fig. 1-e) forming flag-like process. As a result, branchiae and notopodial lobes seem to be fused only at base. Branchiae became of nearly equal size with postsetal notopodial lobes from setiger 17-28, which gradually decreased in size to the posterior end of body. Posterior notopodial lamellae small and oval. Neuropodial lamellae of anterior 14-20 setigers are wide and high, rectangular with rounded margins. Width of inferior half of neuropodial lamellae decreases from setiger 15-21 (Fig. 1-e). Hooks situated beneath neuropodial lamellae from setiger 17-23. Notopodia shifted dorsally from setiger 16-28. Segments become longer after setiger 16-21.

Setiger 1 lacks notosetae. Sabre setae or inferior neuropodial fascicle of setae absent. Neuropodial hooded hooks from setiger 14-18; up to 14 per fascicle, but reaching this number only in largest specimens and in a few segments (1-3) usually from segment 10-15 after starting of hooks. There are three teeth in hooks (in lateral view), and four teeth (in frontal view): highest tooth paired as a rule (Fig. 1g-h). Secondary hood absent. Notopodial hooded hooks absent. Notopodial capillaries become longer after setiger 14-19.

Pygidium with oval more or less flattened, slightly bilobed ventral cushion (Fig. 1-f).

PIGMENTATION. — None.

REMARKS. — The shape of prostomium and the shape of hook in lateral view, the setiger where neuropodial hooks begin and the presence of a notch on notopodial postsetal lobe makes this species close to *Scolelepis tridentata* (Southern, 1914). However the absence of an inferior fascicle in the neuropodium and the characteristic outline of hook's hood, the presence of four-teeth hooks with different arrangement of apical teeth separated this taxon from *S. tridentata* (LIGHT, 1977, 1978). The absence of notosetae on setiger 1 (SOUTHERN, 1914) would have been similar as in *S. tridentata* and *S. korsuni*, but LIGHT (1978) reported after studying type material of *S. tridentata* that the syntypes do have notopodial fascicle on setiger 1.

Fused branchiae and postsetal notopodial lobes form superior flag-like process in the middle of body so some researchers may think this species is equal to *S. gilchristi* (DAY, 1961) or *S. geniculata* Imajima, 1992, but *S. gilchristi* and *S. geniculata* have notosetae on setiger 1 whereas *S. korsuni* does not.

This species is also close to *S. quinquedentata* (HARTMANN-SCHRÖDER, 1965), *S. papillosus* (OKUDA, 1937) and *S. texana* Foster, 1971. *S. quinquedentata* differs in the shape of hooks, the number of hooks per neuropodium, notopodial lobes shorter than branchiae, anterior and posterior eyespots of different shape. *S. papillosus* has entire notopodial lobes on at least 42 anterior setigers with up to 18 hooks per neuropodium. *S. texana* differs in the shape of hooks, entire notopodial lobes on anterior 30 setigers and a number of hooks per neuropodium.

ETYMOLOGY. — This species is named for Dr. Sergey A. KORSUN, Marine Biological Institution of Murmansk. He is a specialist on Foraminifera and my good friend.

### *Scolelepis burkovskii* sp.nov.

MATERIAL EXAMINED. — Barents Sea. R/V "Pomor": stn 17.5b, 69°08'N, 50°22'E, 19 m, sand, 4.30°C, 16.VII.1985, grab 1: holotype (ZMUM Pl 821) and three paratypes (ZMUM Pl 822); grab 2: two paratypes (ZMUM PL 823 and ZMUC).

DESCRIPTION. — Maximum length - 8-9 mm; maximum width - 0,6 mm. The single complete specimen had 50 setigers. Figs 1 i-p.

Prostomium anteriorly pointed with an approximately right angle (Fig. 1-i). Caruncle narrow and pointed, extending posteriorly to the middle of setiger 2. Two pairs of eyespots. Occipital crest not pronounced. Occipital

Source : MNHN, Paris

tentacle absent. Palps without basal sheath (present in only the holotype) reaching posteriorly to setiger 6-7. Peristomium without lateral wings.

Branchiae flattened, partly fused basally with notopodial lamellae. Branchiae of setiger 2 approximately 1.5 times longer than notopodial lamellae. On the following setigers the ratio increases to 2 or 3 times (Figs 1 k-l). Branchiae continuing throughout body, but becoming progressively smaller in posterior third of body with the upper margins becoming of equal length with notopodial lamellae in the last setigers.

Notopodial lamellae of several anterior setigers slightly elongated becoming more or less semicircular in the following setigers. Neuropodial lamellae of setiger 1 small and low lamellae becoming higher and semicircular in the following setigers; they are slightly asymmetrical anteriorly with a wide dorsal half (Fig. 1-j). Notch on neuropodial lamellae absent.

Setiger 1 with notosetae (Fig. 1-j). An inferior fascicle of capillary setae present in the neuropodium in all setigers (sabre setae absent). Notopodial fascicle becomes narrow posteriorly consisting of a small number of capillaries (Fig. 1-m). Neuropodial hooks from setiger 17-19, numbering 6-8 per fascicle ; hooks tridentate with pair of widely arranged apical teeth surmounting main tooth (Figs 1 o-p). Notopodial hooks absent.

Pygidium with the scalloped membrane surrounding terminal anus.

PIGMENTATION. — Medial longitudinal narrow dark strip present from the anterior margin of prostomium to behind the posterior pair of eyes. In addition, several small spots may be present behind eyes forming 2 dark fields connected with a longitudinal strip (Fig. 1-i).

REMARKS. — This species may be confused with *Spio theeli* (SÖDERSTRÖM, 1920) in habiting in the same area. MACIOLEK (1987) placed *Microspio theeli* into *Scolelepis* but this species does belong to *Spio*-genus group. The new species can be separated by the shape of the hooded hook and the absence of sabre setae in inferior fascicle of neuropodium. I attribute this species to *Scolelepis* because of the shape of pygidium and prostomium, the absence of segmented nuchal organ and the absence of sabre setae. This species differs from the other species of genus *Scolelepis* by starting of hooded hooks, shape of hooks, prostomium, parapodial lobes and composition of setae in neuropodia.

ETYMOLOGY. — The species is named in honour of Professor Igor V. BURKOVSKI who was my principal advisor of my Ph. D. Thesis.

### *Scolelepis matsugae* sp.nov.

MATERIAL EXAMINED. — Barents Sea. Drozdovka Inlet. Exp. of Murmansk Marine Biological Instution, coll. A.V.SIKORSKI: stn P1, 68°18'20"N, 38°25'E, grab, 7.5 m, sandy silt with detritus, 17.VIII.1984: holotype (ZMUM Pl 818). Franz Josef Land. Hayes Isl. Exp. ZIN, coll. V.G.AVERINTSEV & A.F.PUSHKIN: stns 22, 40, 43, 44, 54, 73, 83; 80°35'N, 57°50'E, 3-7 m, silt and in *Alaria esculenta* on stones, X-XII.1981: 10 paratypes (ZMUM Pl 819 and Pl 820; ZIN 2/47388-8/47394; one specimen in ZMUC). Kara Sea. R/V "Zarja", coll. Russian Polar Exp.: stn 12d, 74°28'N, 83°33'E, 52 m, thin clay, 19.VIII.1900: one paratype (ZIN 1/47387).

DESCRIPTION. — Holotype complete, 1.7 mm wide and 9.5 mm long for 48 setigers; maximal number of setigers 50; largest specimen incomplete, 2.8 mm wide. Figs 2a-k.

Prostomium with three semicircular anterior projections (Fig. 2-a); middle projection, especially in juveniles, less prominent than the lateral ones (Fig. 2-c) ; occipital crest high, well pronounced, posteriorly ending abruptly; caruncle ending at base of setiger 1; two pairs of eyes present, with anterior pair larger, crescent-shaped and further apart spaced than posterior pair. Longitudinal groove on prostomium well developed in adults, and extend from the base of occipital crest to the anterior margin around middle projection. Peristomium large in comparison to prostomium, high, laterally inflated. Pharynx often more or less eversed, resulting in anterior margin of prostomium being abruptly turned dorsally. Peristomium distinct from setiger 1, lateral wings lacking; palps thick, long, without basal sheath extending posteriorly to setiger 14.

Setiger 1 without notosetae but with notopodial lamellae. Branchiae flattened, fused entirely to wide Setiger 1 without notosetae but with notopodial lamellae. Branchiae flattened, fused entirely to wide notopodial lamellae. Branchiae of setiger 2 are well developed, long and only 1.5 times shorter than longest one on setiger 14 or 15; fused branchiae and notopodial lamellae abruptly diminished on setiger 22-29, becoming low, semicircular and not changing in shape and size posteriorly.

Source : MNHN, Paris

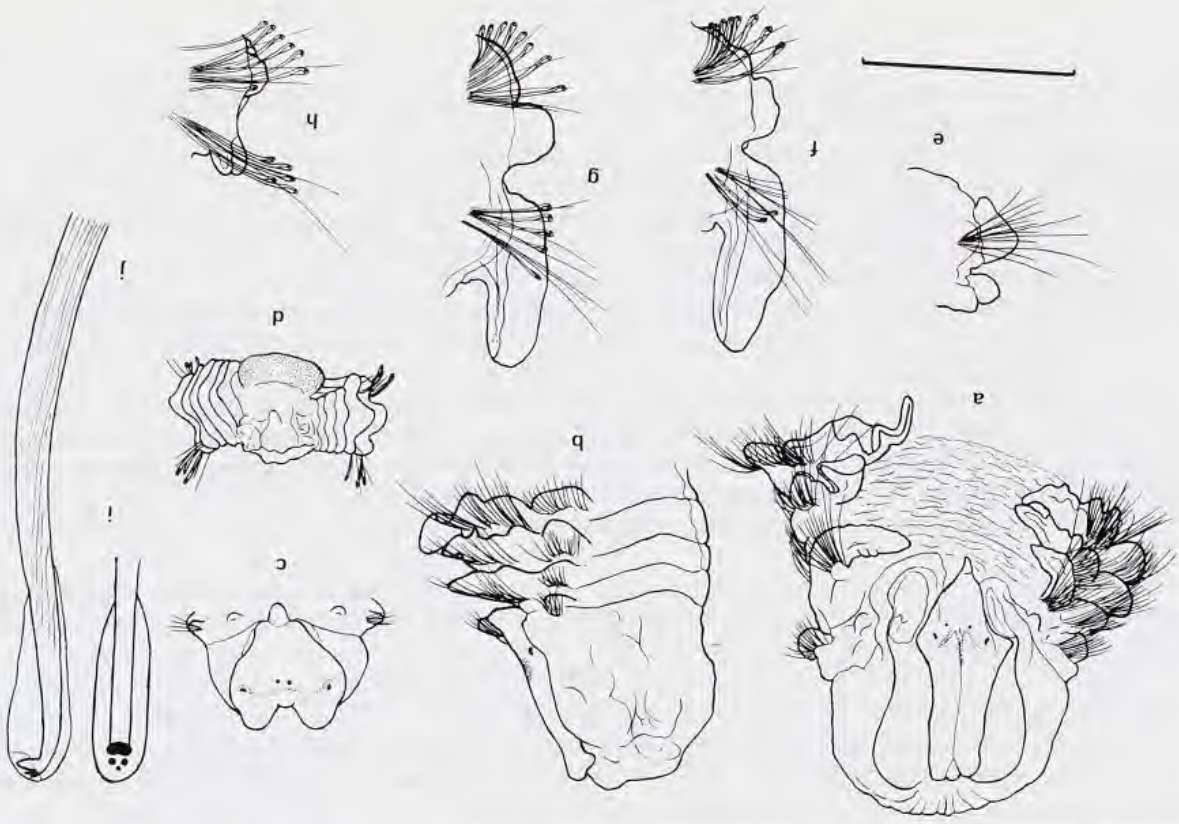


FIG. 2. — *Scolelepis matsugae* sp. nov.: a, anterior end through first four setigers, in dorsal view (palps missing). b, same anterior end, in lateral view. c, anterior end of juvenille specimen, in dorsal view. d, pygidium. e, first parapodium. f, parapodium 23. g, parapodium 25. h, parapodium 36. i, distal end of a hooded hook (in frontal view scheme). - j, a hooded hook from parapodium 25, in lateral view. Scale: a and b, 1 mm; c, 0.3 mm; d, 0.8 mm; e-h, 0.5 mm; j, 0.035 mm.

Neuropodial postsetal lamellae of anterior setigers irregularly rounded, with notch starting from setiger 16-18; ventral parts of neuropodial postsetal lamellae on following segments reduced, resembling narrow membrane and absent on posterior setigers. Almost all neuropodial fascicles of anterior half of body shorter than the upper part of neuropodial postsetal lamellae. Superior notopodial capillares of anterior setigers longest. Sabre setae or inferior fascicle of neuropodium absent. Neuropodial hooks present from setiger 11-22, numbering up to 9 per fascicle. Only young specimens (≤ 0.5 mm width) have hooks from setiger 11-13. Shedding of hooks connected with age confirmed by presence of one hook in neuropodium 14 of holotype; the next neuropodium with hooks in the holotype was in setiger 17. Notopodial hooded hooks begin at setigers 13-26, numbering up to 5 per fascicle. Hooks are tridentate in side view, but in frontal view main tooth clearly surmounted by pair of apical teeth and a single, unpaired (Figs 2 i-j).

Anus terminal, sometimes slightly displaced to dorsum (Fig. 2h). Pygidium with ventral transverse cushion.

PIGMENTATION. — A slight dark stripe present along posterior part of longitudinal groove on prostomium with two dispersing stripes in front of eyes (Fig. 2-a). One juvenile specimen with transverse dark stripes behind anterior pair of eyes (Fig. 2-c). Proximal part of eversed pharynx usually with dark ring. One specimen with pigment on tip of notopodial postsetal lamellae on setiger 3. Anal cushion pigmented. Palps with diffused pigment.

REMARKS. — This species resembles *Scolelepis oligobranchus* (CHLEBOVITSCH, 1959). However, *S. matsugae* differs from *S. oligobranchus* in its smaller size, fused branchiae and notopodial postsetal lamellae reduced more anteriorly, absence of an inferior fascicle of neuropodium, shape of pygidium and shape of hooks. Hooks of *S. oligobranchus* are bifid in side view but their apical tooth paired; it had not been mentioned in original description but it is clearly visible in the holotype.

Source : MNHN, Paris

ETYMOLOGY. — The species is named for my mother Nina Pavlovna SIKORSKA. Her maiden name was MATSUGA.

There are now five valid species of genus *Scolelepis* known from the Arctic Ocean.

Key to species of *Scolelepis* from the Arctic Ocean

| | | |
|---|---|---|
| **1** | Prostomium pointed anteriorly | **2** |
| | Prostomium rounded or trifid anteriorly | **4** |
| **2** | Anterior branchiae completely fused to dorsal lamellae; setiger 1 without notosetae | *S. korsuni* |
| | Anterior branchiae free distally; setiger 1 with notosetae | **3** |
| **3** | Neuropodial hooks from setiger 17-19; ventral lamellae without notch; notopodial hooded hooks absent | *S. burkovskii* |
| | Neuropodial hooks from setiger 26-42; ventral lamellae with a notch after setiger 18-20; notopodial hooks from setiger 60-75 | *S. squamatus* |
| **4** | Neuropodial hooks from setiger 11-22; branchiae become very short abruptly on setiger 22-29 | *S. matsugae* |
| | Neuropodial hooks from setiger 50-67; branchiae diminish gradually becoming very short near end of body | *S. foliosus* |

## ACKNOWLEDGEMENTS

I would like to thank Drs. I.A. JIRKOV, M.A. SAFRONOVA, A.B. TZETLIN for reviewing the manuscript ; M.V. KOLESNIKOV, A.K. KARAMYSHEV, Drs. V.G. AVERINTSEV, A.F. PUSHKIN, N.A. ANISIMOVA, the consulting firm Akvaplan-niva and Elf Aquitaine Norge AS for helping in collectioning the specimens. I am especially grateful to the referees of the manuscript for their critical review and to Dr. M.E. PETERSEN for valuable advise.

## REFERENCES

BLAKE, J.A. & KUDENOV, J.D, 1978. — The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. *Mem. Nat. Mus. Victoria*, **39** : 171-280.

BLAINVILLE, H. de, 1828. — *Dictionnaire des Sciences naturelles*. **57** : 368-501.

CHLEBOVITSCH, V.V., 1959. — Species of polychaete worms from the Kuril Islands, which are new or recorded for the first time on the USSR (Leningrad). *Zool. Zh.*, **38** : 167-181 (in Russian).

DAY, J.H., 1961. — The polychaete fauna of South Africa. Part 6. Sedentary species dredged off Cape coasts with a few new records from the shore. *J. Linn. Soc. Zool.*, **44** : 463-560.

FOSTER, N.M., 1971. — Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. *Stud. Fauna Curaçao*, **36** : 1-183.

HANNERZ, L., 1956. — Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden). *Zool. Bidr. Uppsala*, **31** : 1-204.

HARTMANN-SCHRÖDER, G., 1965. — Die Polychaeten des Sublitorals. *In* : G. HARTMANN-SCHRÖDER & G. HARTMANN (eds.), Zur Kenntnis des Eulittorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitt. hamb. zool. Mus. Inst.*, Suppl. **62** : 59-305.

HARTMANN-SCHRÖDER, G., 1971. — Annelida, Borstenwürmer, Polychaeta. *Die Tierwelt Deutschlands*, **58** : 1-594.

IMAJIMA, M., 1992. — Spionidae (Annelida, Polychaeta) from Japan VIII. The genus *Scolelepis*. *Bull. Natn. Sci. Mus. Tokyo*, Ser.A, **18** : 1-34.

KIRKEGAARD, J.B., 1969. — A quantitative investigation of the central North Sea. *Spolia*, **29** : 8-285.

Source : MNHN, Paris

LIGHT, W.J., 1977. — Spionidae (Polychaeta; Annelida) from San Francisco Bay, California: a revised list with nomenclatural changes, new records, and comments on related species from the northeastern Pacific Ocean. *Proc. Biol. Soc. Wash.*, **90** : 66-88.

LIGHT, W.J., 1978. — *Spionidae (Polychaeta; Annelida)*. Invertebrates of the San Francisco Bay Estuary System, Pacific Grove, California, 211 pp.

MACIOLEK, N.J., 1987. — New species and records of *Scolelepis* (Polychaeta: Spionidae) from the east cost of North America, with a review of the subgenera. *Bull. Biol. Soc. Wash.*, **7** : 16-40.

MESNIL, F., 1896. — Études de morphologie externe chez les Annélides. Les Spionidiens des côtes de la Manche. *Bull. Sci. France Belg.*, sér.4., **29** : 110-287.

OKUDA, S., 1937. — Spioniform polychaetes from Japan. *J. Fac. Sci. Hokkaido Univ.*, Ser. 6, Zool **5** : 217-254.

SARS, M., 1851. — Beretning om en i Sommeren 1849 foretagen zoologisk Reise i Lofoten og Finmarken. *Nyt Mag. Naturv. Oslo*, **6** : 121-211.

SARS, M., 1873. — Bidrag til Kundskaben om Norges Annelider. *Vidensk. Selsk. Christiania, Forh.* : 1-51.

SÖDERSTRÖM, A., 1920. — *Studien über die Polychäten-familie Spionidae*. Dissertation, Uppsala, 286 pp.

SOUTHERN, R., 1914. — Archiannelida and Polychaeta. *Roy. Irish Acad. Dublin.*, **31** : 1-160.

WESENBERG-LUND, E., 1951. — Polychaeta. *Zoology Iceland*, **2** : 1-182.

Source : MNHN, Paris

# A systematic problem of inter- and intra-generic variation in nephromixia of Terebellidae

*Ralph I. SMITH*

Department of integrative Biology
University of California
Berkeley, California, 94720, U.S.A.

ABSTRACT

The nephromixial systems of *Pista fimbriata* Moore, 1923 (a typical *Pista*) and of two aberrant "*Pista*", *P. elongata* Moore, 1909 and *P. pacifica* Berkeley & Berkeley, 1942, are described. The latter two species do not belong in *Pista*, but no described genus can accomodate them. If they are congeneric, the differences between their reproductive nephromixia exceed any intra-generic variation previously reported in the nephromixial system of any terebellid genus. Some taxonomic and phylogenetic implications are discussed.

RÉSUMÉ

**Un problème systématique de variabilité inter- et intra-générique dans la néphromixie des Terebellidae**

Les systèmes néphromixiaux de *Pista fimbriata* Moore, 1923 (une *Pista* typique) et de deux "*Pista*" aberrantes, *P. elongata* Moore, 1909 et *P. pacifica* Berkeley & Berkeley, 1942, sont décrits. Les deux dernières espèces n'appartiennent pas au genre *Pista*, ni à aucun autre genre connu. Si elles sont congénériques, les différences entre leurs nephromixies reproductrices surpassent toutes les variations intragénériques décrites parmi les genres de térébellides. Quelques implications taxonomiques et phylogénétiques sont discutées.

Nephromixia (GOODRICH, 1895, 1945; SMITH, 1988) are complex segmental organs serving excretory and reproductive fonctions. Their morphology show great inter-generic variations in the Terebellidae (MEYER, 1887; HESSLE, 1917; SMITH, 1989), but intra-generic variation in these organs has not previously been described. The study reported herein is the subject of a longer and fully-illustrated paper in the Journal of Morphology (SMITH, 1992). Most of the illustrations used in the oral presentation at this Conference will be found in that paper and so will not be reproduced here. Reprints will be furnished to Conference participants upon requests.

Two Californian species, *Pista elongata* Moore, 1909 and *P. pacifica* Berkeley & Berkeley, 1942, have been found to differ markedly in nephromixia and other respects from typical *Pista*, type *P. cristata* (O.F. Müller,1776). *Pista fimbriata* Moore, 1923 are described and illustrated, and it is confirmed that typical *Pista* (insofar as has

SMITH, R.I., 1994. — A systematic problem of inter- and intra-generic variation in nephromixia of Terebellidae. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 287-289. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

Typical *Pista* is characterized by two, often unequal, pairs of dendritic branchiae, prominent lateral lappets, and especially by distinctive crested, long-handled, avicular, anterior uncini. In the present study the nephromixia of been reported) has one pair of anterior, pre-septal, non-reproductive, "excretory" nephromixia (ENMX) opening by obscure "renal" apertures on segment III. Post-septally occur two pairs of reproductive nephromixia (RNMX) that open on genital papillae located dorsally, just posterior to the notopodia of segments VI and VII. These RNMX are not united by lateral common ducts (Figs 1B, E). The tubes of *Pista* are usually reported as thick-walled and muddy, without apertural ornamentation.

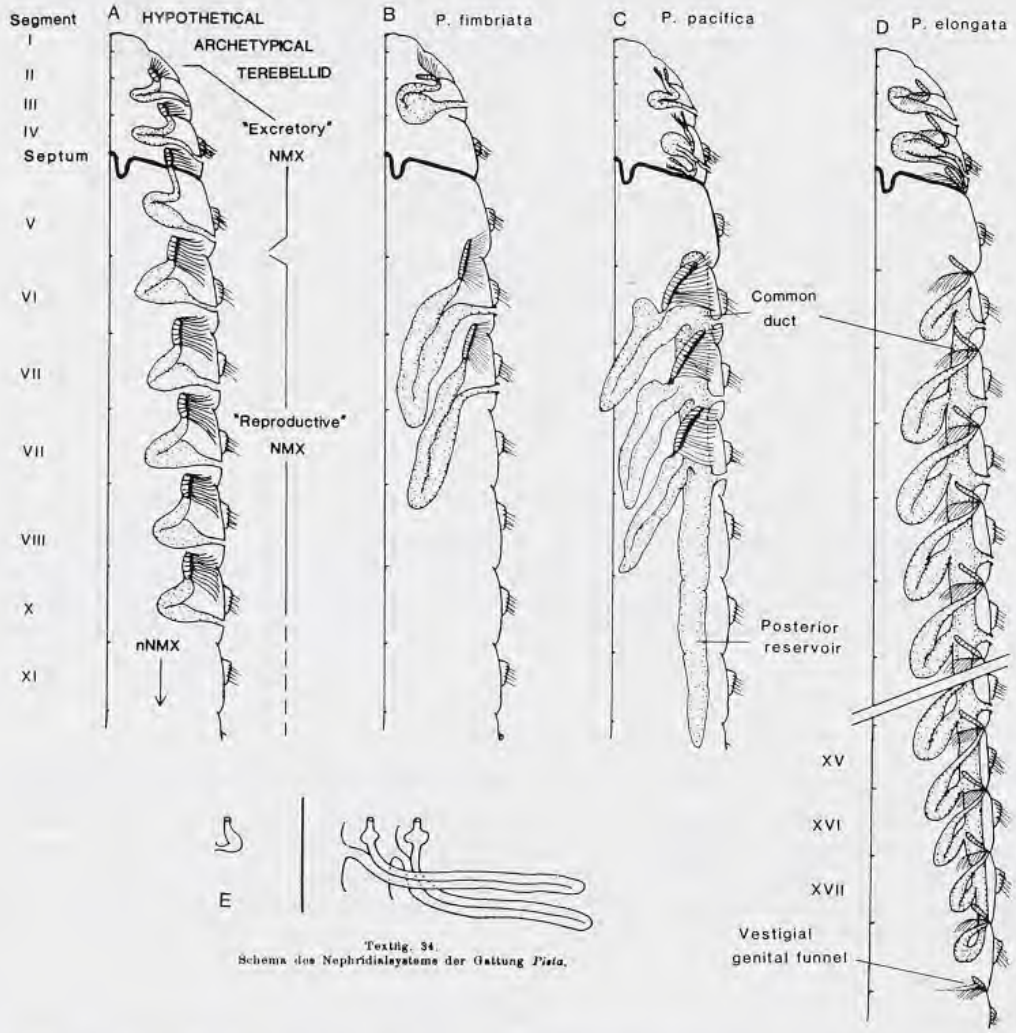



FIG. 1. — A-D, "Procrustacean Bed" representation of nephromixial systems of an hypothetical archetypical terebellid and of *Pista fimbriata* Moore, *P. pacifica* Berkeley & Berkeley, and *P. elongata* Moore. The nephromixia are fitted into a common bed for comparison. E, HESSLE's schema of the nephromixial system of *Pista*.

In contrast, *Pista pacifica* is easily recognized in its habitat in muddy sand flats by its long, chitinous, sandy, vertical tube with a distinctive fringed hood at the surface aperture and a button-like plaque with a cross-shaped slit at its lower end. *Pista pacifica* has lappets and its anterior uncini are long-handled, but are stout and crochet-like, unlike those of typical *Pista*. It differs most markedly from typical *Pista* in its nephromixia (Fig. 1C). There are two pairs of ENMX but three pairs of ciliated renal funnels. The first pair of funnels supply a pair of ENMX opening by papillae at the tops of the second lappets (segment III). The second and third pair of funnels supply the second ENMX, which open by papillae on the third lappets (segment IV). Post-septally, are three pairs of large

Source : MNHN, Paris

and complex RNMX, those on each side united by a lateral common duct with posterior extension, and discharging by obscure genital papillae on segments VI, VII and VIII.

*Pista elongata* occupies rock crevices and pholad bore-holes. Its tough, membranous, sand-encrusted tube opens within a bilobed reticulated hood. It is pointed out that the morphology of such tubes is often as specifically distinct as other morphological characteristics, as much as is a gastropod shell, and should be included in specific descriptions. *P. elongata* has long-handled anterior crochet-like uncini indistinguishable from those of *P. pacifica*. Likewise, it has been the same arrangement of ENMX, three pairs of ciliated funels supplying two pairs of ENMX opening on lappets of segments III and IV. But it differs from *P. pacifica* in having 9-11 pairs of relatively simple RNMX united on each side by a common duct (Fig. 1D). The number of RNMX exceeds the number of genital papillae, and small, vestigial, genital funnels may occur posterior to the common ducts. This suggests that the posterior extensions of the common ducts seen in *P. pacifica*, as well as in certain other species, may have resulted from the losse of the more posterior RNMX in evolution.

HESSLE (1917) has shown that nephromiwia of terebellid polychaetes exhibit great inter-generic variation, but he suggested little or no intra-generic variation. The differences between *P. pacifica* and *P. elongata* on the one hand and typical *Pista* on the other in respect to anterior uncini, tube morphology, and in ENMX and RNMX are sufficient to justify removal of the two former species from *Pista* but, on present information, no described genus can accomodate them. Further, the differences in RNMX between these species is a great as might characterize separate genera, although on the bases of branchiae, lappets, tubes, anterior uncini, and ENMX they appear congeneric. The differences in RNMX represent a degree of intra-generic variation not previously reported in the Terebellidae. Possibly the patterns of ENMX here demonstrated are only the extremes of intra-generic variation, in which intermediate patterns may have been lost or not yet discovered. Might sub-generic status be justified? Paradoxically, an "intermediate" condition of the RNMX is shown by *Lanice conchilega*, which has four pairs of RNMX joined by common ducts, but in this species the anterior uncini are of an entirely different avicular form, and the ENMX differ as well (MEYER, 1887). Nephromixial patterns seem to have evolved quite independently of the form of the uncini, and the similarity between the latter might represent convergent adaptations to life in comparable tubes.

The information implicit in the diverse patterns of nephromixial morphology in terebellid polychaetes may be useful in phylogenetic studies, and should be included whenever possible in specific descriptions within the Terebellidae.

## REFERENCES

GOODRICH, E.S., 1895. — On the coelom, genital ducts and nephridia. *Q. J. micr. Sci.*, **37** : 253-267.

GOODRICH, E.S., 1945. — The study of nephridia and genital ducts since 1895. *Q. J. micr. Sci.*, N.S., **86** : 113-392.

HESSLE, C., 1917. — Zur Kenntniss der terebellomorphen Polychaeten. *Zool. Bidrag fran Uppsala*, **5** : 39-258.

MEYER, E., 1887. — Studien über der Korperbau der Anneliden, I-III. *Mitth. Zool. Sta. Neapel*, **7** : 592-741.

SMITH, R.I., 1988. — Mixonephridia or nephromixia in terebellid polychaetes? A clarification. *Comp. Biochem. Physiol.*, **91C** : 265-272.

SMITH, R.I., 1989. — Observations on spawning behavior of *Eupolymnia nebulosa* and comparisons with *Lanice conchilega* (Annelida, Polychaeta, Terebellidae). *Bull. mar. Sci.*, **45** : 406-414.

SMITH, R.I., 1992. — Three nephromixial patterns in polychaete species currently assigned to the genus *Pista* (Annelida, Terebellidae). *J. Morph.*, **213** : 365-393.

Source : MNHN, Paris

Source : MNHN, Paris

# Morphometric variation in bifurcate notosetae of two *Euphrosine* species (Polychaeta, Euphrosinidae)

*Ken D.VOGT & Jerry D. KUDENOV*

Department of Biological Sciences
University of Alaska Anchorage
3211 Providence Drive
Anchorage, Alaska 99508 U.S.A.

ABSTRACT

Univariate and multivariate analysis of covariance based on four morphological factors reveal that prong lengths and ratios of bifurcate notosetae in two *Euphrosine* species (Polychaeta, Euphrosinidae) vary systematically along both the body axis and within setal fascicles in relation to body size. Body size was measured as a function of two covariates: total numbers of segments and body weights. Principle component analysis revealed that the majority of notosetal variation in these species is attributable to body size ; the remainder to setal position within notofascicles. Discriminant analysis correctly distinguished between the notosetae of these species in nearly all cases. These preliminary results tend to validate the traditional use of prong lengths and ratios to describe the bifurcate notosetae of euphrosinids.

RÉSUMÉ

**Variation morphométrique des soies dorsales bifurquées de deux espèces d'*Euphrosine* (Polychète, Euphrosinidae)**

Les analyses univariées et multivariées de la covariance basée sur quatre caractères morphologiques révèlent que la longueur des branches des soies fourchues et les proportions des soies notopodiales bifides des deux espèces d'*Euphrosine* (Polychètes, Euphrosinidae) varient selon leur position dans l'axe du corps et avec les fascicules des soies en relation avec la taille du corps. La taille du corps a été mesurée comme une fonction de deux variables liées : le nombre total de segments et le poids du corps. L'analyse en composantes principales montre que la variation majeure des soies notopodiales de ces espèces est liée à la taille du corps ; les autres variations sont liées à la position dans les faisceaux dorsaux. L'analyse discriminante permet de distinguer correctement, dans tous les cas, les soies notopodiales des espèces. Ces résultats préliminaires proposent la validation de l'utilisation traditionnelle des longueurs des branches des soies fourchues et de leur proportion pour décrire les soies notopodiales bifides des euphrosinides.

## INTRODUCTION

Although the setae of polychaetous annelids are generally recognized to be highly variable morphological traits that vary over time and space (FAUCHALD, 1991), morphometric studies on setal variation have only recently

VOGT, K.D. & J.D. KUDENOV, 1994. — Morphometric variation in bifurcate notosetae of two *Euphrosine* species (Polychaeta, Euphrosinidae) *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 291-298. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

begun (GAFFNEY, 1973; GARWOOD & OLIVE, 1981; BHAUD, 1983; ORRHAGE & SUNDBERG, 1990; FAUCHALD, 1991, 1992). The need to incorporate such data into polychaete systematics is critical since: 1) simple linkages between morphology and the distinctions between biological species probably do not exist (GRASSLE & GRASSLE, 1976; LEVIN, 1984; ORRHAGE & SUNDBERG, 1990) ; 2) systematically significant morphological variation exists in species previously considered to be cosmopolitan or widely distributed (HARTLEY, 1984; WILLIAMS, 1984); and 3) setal morphology may be variously influenced by combinations of environmental factors as has been documented in oligochaetes (SCHROEDER, 1984; CHAPMAN & BRINKHURST, 1987, but see GAFFNEY, 1973).

There have been no quantitative studies of setae published on the Order Amphinomida, although setal variation has been noted (MOORE, 1905; HORST, 1912), and GUSTAFSON (1930) illustrated the kinds of setae present in the genera included in his study. KUDENOV (1987) suggested that bifurcate notosetae should be studied quantitatively to validate their use in the systematics of *Euphrosine*. This paper reports preliminary findings on morphometric variation of the bifurcate notosetae in two species of *Euphrosine*: *E. borealis* Öersted, 1843 and *E. bicirrata* (Moore, 1905). Work continues on morphometry of neurosetal variation and will be reported elsewhere.

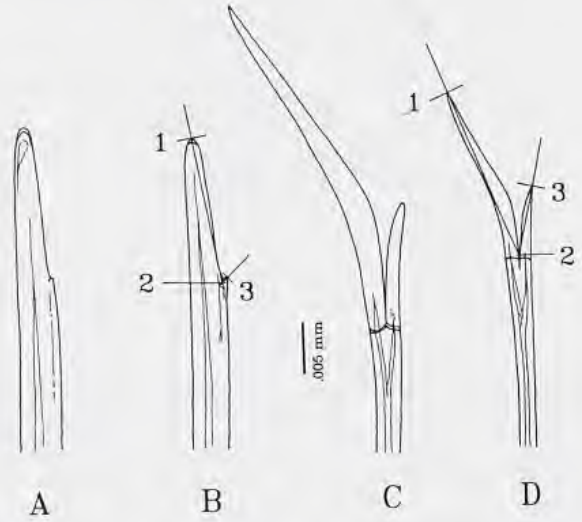



FIG. 1. — Prong lengths of bifurcate notosetae of *Euphrosine borealis* (A, B) and *E. bicirrata* (C, D), involving measurements between points 1-2 for long prongs, and points 2-3 for short prongs. A, C, superior notosetae. B, D, inferior notosetae.

## MATERIALS AND METHODS

In all, 15 preserved, complete specimens (four of *E. bicirrata*; 11 of *E. borealis*) examined as part of this study were obtained on loan through the Department of Biology, Moscow State University, and the P.P. Shirshov Institute of Oceanology. Unfortunately, locality data have not yet been made available.

A two stage stratified sampling routine was used in which setae were collected from the top and bottom of notosetal fascicles of anterior (setiger 6), middle (14-18), and posterior (24-30) body regions. Setal measurements include long prong length (LP) and short prong length (SP) (Fig. 1); long to short prong ratios (LP/SP) were calculated. Abbreviations are used as subscripts for probability values given below. All setal measurements were made at 400 times magnification, and repeated nonconsecutively. Body size was estimated using two covariates: total numbers of setigers (S) and body weight (W). Body weights, recorded as wet weights of specimens stored in alcohol, were measured using an analytical balance.

Statistical analyses (Analysis of Covariance [ANCOVA] : MONTGOMERY, 1984; Multiple Analysis of Covariance [MANCOVA]: MANLY, 1990) were carried out for natural-, square root- and $\log_e$-transformed data. Confirmation of normality was prerequisite to all parametric tests used (MONTGOMERY, 1984; MANLY, 1990). Nonparametric uni-and multivariate tests were used for *E. borealis* data that could not be normalized (CONOVER, 1980). Principal component analysis was calculated for both species (MANLY, 1990). Discriminant analysis of prong lengths and ratios for both species was constrained to a nonparametric multivariate test (K-NEAREST

Source : MNHN, Paris

NEIGHBOR: HAND, 1989) on prong lengths and ratios vs. body size and fascicle position for both species since *E. borealis* data could not be normalized. K values (1-5) were used initially for both species ; those for which the fewest misidentifications occurred were selected for further analysis. Blocks for anterior, middle and posterior body regions for all statistical tests were taken to represent total numbers of segments.

Statistical software packages used for all ANCOVA and MANCOVA analyses are found in Statistical Packages for the Social Sciences, version 4.0 (SPSS Inc., 1990) and Statistical Analyses Software, version 6.06 (SAS INSTITUTE Inc., 1990). Probability limits were set at P = 0.05.

## RESULTS

In all, 953 notosetae were measured (432 from four *E. bicirrata*; 521 from 11 *E. borealis*). In *E. bicirrata*, body segment numbers and body weights ranged from 24-31 and from 0.117-0.129 g, respectively; in *E. borealis* they ranged from 23-41 and 0.06-2.7 g. Results of statistical analyses for both species reveals the presence of continuous and verifiable variation both along the body axis and within notopodial fascicles.

### The notosetae of *Euphrosine bicirrata*

Within-cell MANCOVA treatment of prong lengths vs body size and setal position within fascicles reveals the lengths of both prongs simultaneously increase from the top to bottom of a fascicle (MANCOVA: Fig. 2a-b, $P_{LP} = P_{SP} = 0.002$, Wilkes-lambda = 0.08) and along the length of the worm as body size increases (MANCOVA: Fig. 2a-b, $P_S = P_W = 0.002$, Wilkes-lambda = 0.08). Although long prongs appear to increase in length, they were found to vary independently of body size when tested alone (MANCOVA: Fig. 2c, $P_S = .062$, $P_W = 0.072$). In contrast, short prongs directly influence this multivariate association when examined separately. Short prongs increase in length towards posterior segments as body size increases (MANCOVA: Fig. 2d, $P_S = P_W = 002$, Wilkes-lambda = 0.08).

Partial cell MANCOVA treatment of prong lengths vs fascicle position (holding the influence of body size constant), reveals that both prongs increase in length from the top to bottom of fascicles (MANCOVA: $P_{LP} = P_{SP} = .002$, Wilkes-lambda= 0.07),

$Log_e$-transformed ratios of prong lengths decrease from top to bottom of notofascicles (ANCOVA: $P_{LP/SP} = 0.025$) and along the length of the worm (ANCOVA: $P_{LP/SP} = 0.005$) as body-size increases. Prong lengths are positively correlated to total body segment numbers (r = +.512, N = 432), and negatively correlated to total body weight (r = -0.531, N = 432).

Principle component analysis disclosed that 91.3 % of total observed variation in this study is explained by body size while the remaining 8.7 % is attributable to setal position within notofascicles.

### The notosetae of *Euphrosine borealis*

In contrast to data obtained for *E. bicirrata*, only the data for prong ratios could be normalized, and analyzed by ANCOVA; univariate analyses of prong lengths were otherwise tested nonparametrically.

Lengths of both long and short prongs, each tested separately, have statistically constant lengths and vary independently of body size (KRUSKAL-WALLIS: Fig. 3a, $P_{LP} = 0.6458$ ; Fig. 3b, $P_{SP} = 0.4059$). However, both long and short prongs, tested separately, increase in length from top to bottom of notofascicles (KRUSKAL-WALLIS: Fig. 4a-b, $P_{LP} < 0.0001$, $P_{SP} = < 0.0001$).

$Log_e$-transformed ratios of prong lengths, normalized through a $log_e$ transformation, decrease from top to bottom of notofascicles (ANCOVA: $P_{LP/SP} = < 0.0001$), and along the length of the worm with increasing numbers of body segments (ANCOVA: $P_{LP/SP} < 0.0001$), and are independent of total body weight (ANCOVA: $P_{LP/SP} = 0.133$). $Log_e$-transformed ratios of prong lengths are also positively correlated to total body segment numbers (r = +0.995, N = 521) and independent of total body weight (r = 0, N = 521).

Principal component analysis revealed that 72.0 % of the total observed variation in this study is accountable by body size while the balance of 28.0 % is associated with setal positions within notofascicles.

### Discriminant analysis of *Euphrosine bicirrata* and *E. borealis*

The fewest number of notosetal misidentifications for both species occurred when K = 3. A total of four notosetae (two from each species) were incorrectly assigned to the other species. None had any body axis or fascicle location in common, and no pattern to these errors could be discerned. In all, 99.6 % (949/953) of all

Source : MNHN, Paris

notosetae were correctly identified on the basis prong lengths of notosetae from known positions within fascicles and segments.

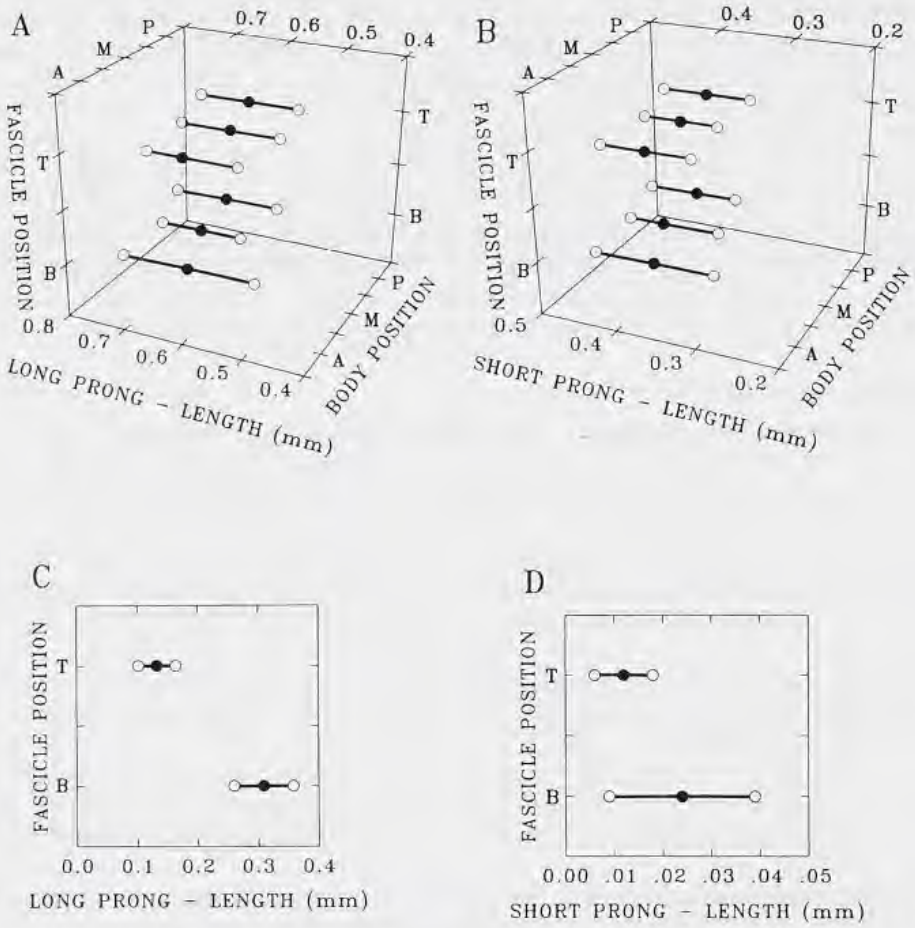



FIG. 2. — *Euphrosine bicirrata* Moore: A, mean length of long prongs from top and bottom of notofascicles along the body axis. B, mean length of short prongs from top and bottom of notofascicles along the body axis. C, mean length of long prongs in relation to position along the body axis (influence of body size removed). D, mean length of short prongs in relation to position along the body axis (influence of body size removed). A, M, P denote anterior, middle and posterior body regions; solid dots represent means; open circles ± 1 standard deviation.

Similar results were obtained for *E. borealis* prong ratios when K = 1 through 4, in that 99.6 % (949/953) of the notosetae in each of four tests were correctly identified; all *E. bicirrata* notosetae were correctly identified.

## DISCUSSION

Bifurcate notosetae of both *Euphrosine bicirrata* and *E. borealis* vary systematically within notofascicles along the length of the body in worms of increasing body size. Few other studies are available that report similar patterns of setae variation along the body of polychaetes. The only work about which we are aware is that of FAUCHALD (1992) which found that total length of setae vary systematically along the body of preserved *Palola* species whereby: 1) all setae are initially short in anteriormost segments, becoming longest in the anterior third, and decreasing gradually in length to the end of the body; 2) setae change from top to bottom of fascicles, and that these patterns vary systematically between species; and that the 3) blades of all compound setae also vary along the body, being longest in middle body segments. Similar, but not necessarily identical, relationships also exist in the bifurcate notosetae of the two *Euphrosine* species examined in the present study. In *E. bicirrata,* prong lengths

Source : MNHN, Paris

simultaneously increase in length from top to bottom of notofascicles in segments along the length of the worm as body size increases. This relationship appears to be controlled more by the length of the short than long prong for

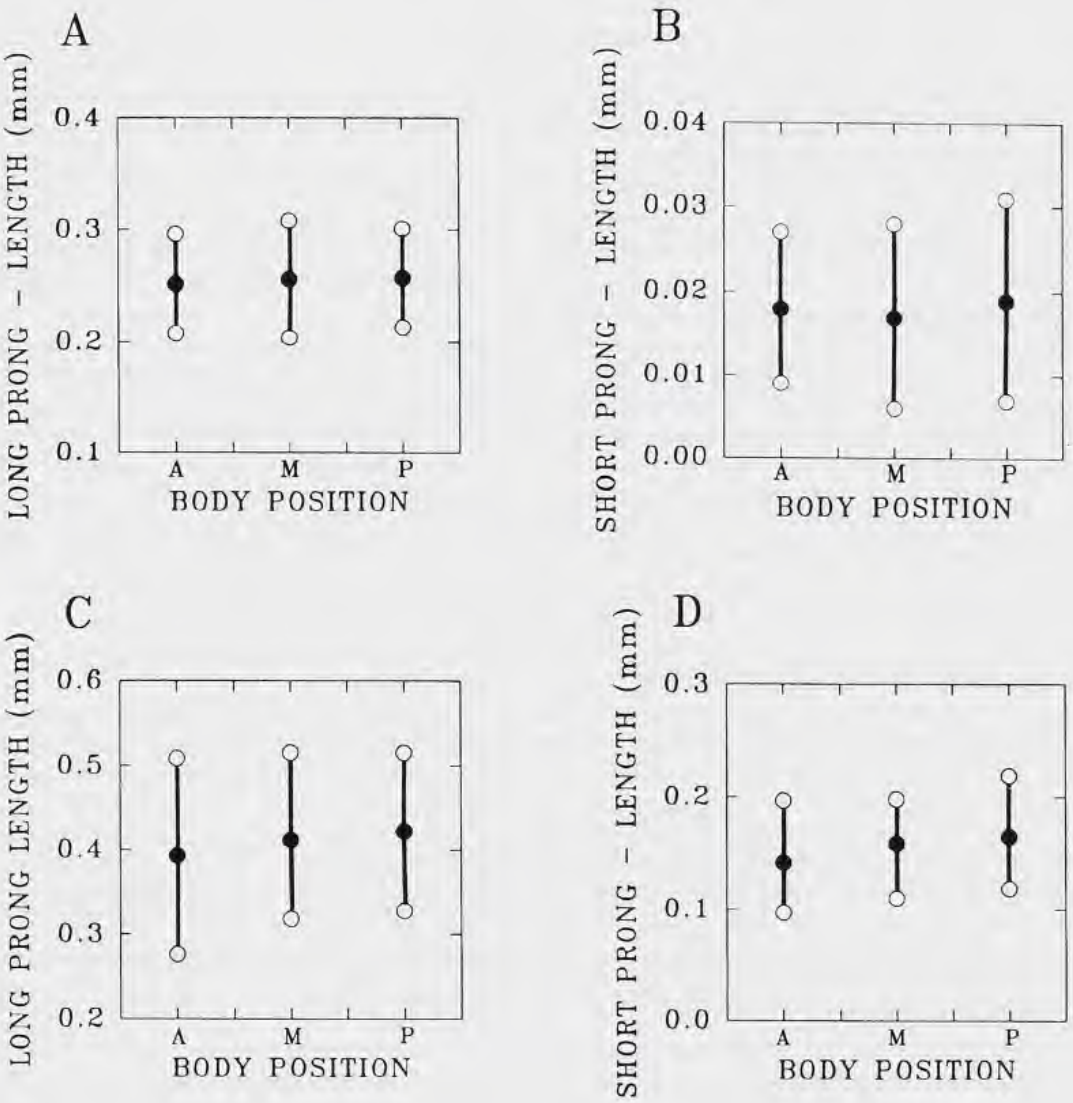



FIG. 3. — *Euphrosine borealis* Öersted: A, mean length of long prongs in relation to position along the body axis. B, mean length of short prongs in relation to position along the body axis. C, mean length of long prongs from top of notofascicles along the body axis. D, mean length of short prongs from bottom of notofascicles along the body axis. A, M, P denote anterior, middle and posterior body regions; T, B denote top and bottom region of notofascicles; solid dots represent mean values; open circles ± 1 standard deviation.

Source : MNHN, Paris

the parameters tested. Variability in the latter may be directly related to some other morphological factor not included in this study. Changes detected in prong lengths within notofascicles are not influenced by size. Prong lengths in *E. borealis* vary independently of body size, and increase from top to bottom of notofascicles.

Little if any biological significance should be attached to these findings when results for *E. bicirrata* and *E. borealis* are compared since the different statistical analyses employed make vastly disparate assumptions about the independent-dependent nature of variables examined (WILLIG *et al.*, 1986; ORRHAGE & SUNDBERG, 1990). For instance, prong lengths are assumed to be dependent variables in euphrosinids since a given seta is generally produced by a single chaetoblast cell in polychaetes (O'CLAIR & CLONEY, 1974; SCHROEDER, 1984; SPECHT, 1988; KRYVI & SORVIG, 1990). Multivariate tests used for *E. bicirrata* recognize the concommitent nature of prong lengths and the influence of body size; univariate tests for *E. borealis* assume all factors to be independent (WILLIG *et al.*, 1986). Moreover, seasonal and ecological variation between samples can not presently be explained until collection data become available.

FAUCHALD (1991) stated that variable morphological traits in eunicids may be: 1) dependent on body size; 2) independent of both body size and other morphological traits; or 3) independent of body size but strongly related to one another. The first two of these relationships apply to results described above from univariate analyses of notosetal prong lengths of *E. borealis*, in which size was assumed to be independent. It may be informative to reconfirm FAUCHALD's results using multivariate techniques.

Natural log-transformed ratios of prong lengths decrease from top to bottom positions of notofascicles and in different segments along the length of the body in both euphrosinids. These ratios decrease along the body axis in both species, but relate differently to one of the two covariates used to estimate body size. For example, ratios change in *E. bicirrata* in relation to increasing body size, and are positively correlated to total segment number, and inversely to body weight; those for *E. borealis* change only in relation and are directly correlated to increasing numbers of segments, being independent of body weight. These correlations probably mirror actual relationships, but caution is again urged against attaching undue significance to these findings for two reasons: 1) body weights were estimated from preserved specimens long stored in alcohol; and 2) sample size, particular for *E. bicirrata*, may have biased the results. Although one seldom has the luxury of examining live or recently preserved euphrosinids, additional specimens of *E. bicirrata* will be examined to address the latter point.

Body size underlies the majority of total notosetal variation in both species, and position of setae within notofascicles accounts for the remaining balance of the two factors studied.

Patterns of both notosetal prong lengths and ratios along the length of the body and within fascicles are highly diagnostic for both *E. bicirrata* and *E. borealis*, provided the locations from which setae are sampled are known and compared using discriminant analysis. Although the process of accumulating these data is laborious, this technique should be used more widely in polychaete systematics.

The use of ratios in biological studies have arithmetic properties which tend to have Cauchy distributions (ROSS, 1988), lack means and variances, and can provide spurious results that are untestable (ATCHLEY *et al.*, 1976). Both ATCHLEY *et al.* (1976) and ATCHLEY & ANDERSON (1978) present statistical arguments opposing the use of ratios in biological studies. Prong ratios describing bifurcate notosetae in euphrosinids seem to reflect expected trends, provided one knows the locations from which setae are derived! However, identifications of *Euphrosine* species should not be based on this character alone, particularly if the body locations are unknown, and a database does not exist.

Setal trends reported above confirm that prong lengths and ratios of bifurcate notosetae in *E. bicirrata* and *E. borealis* vary systematically along the body. Prong lengths and ratios of bifurcate notosetae are here confirmed to be statistically valid characters that have been used traditionally in euphrosinid systematics (KUDENOV, 1987), provided setal locations both within fascicles and along the body axis are known. Euphrosinids should not be identified solely on the basis of bifurcate notosetal prong ratios. It is suggested that future descriptions of euphrosinid taxa include prong lengths and ratios for bifurcate notosetae from the top and bottom of notosetal fascicles from anterior, middle and posterior body segments. However, prior assumptions regarding the systematic importance of prong lengths and ratios should probably not be extrapolated to other *Euphrosine* species until the results of this study are corroborated in other congeners.

## ACKNOWLEDGMENTS

We are indebted to K. FAUCHALD, Smithsonian Institution, for assistance provided, in generously summarizing and sharing the results of his studies on Eunicea, and for commenting on this manuscript. Specimens were kindly made available by I. JIRKOV, Moscow State University, and R. Y. LEVENSTEIN, P.P. Shirshov Institute of

Source : MNHN, Paris

Oceanology, Moscow. Statistical advice was provided by K. THIRUGNANASAMBANTHAN and J. EGENOLF, Dept. of Mathematics, graphics software assistance given by J. KENNISH, Dept. of Chemistry, and R. KULLBERG, Dept. of Biology, University of Alaska Anchorage; assistance with our French abstract was generously provided by D. LACHINSKI. We also thank K. FITZHUGH, Los Angeles County Museum of Natural History, and an anonymous reviewer for helpful comments that improved this paper.

## REFERENCES

ATCHLEY, W.R. & ANDERSON, D. 1978. — Ratios and the statistical analysis of biological data. *Syst. Zool.*, **27** : 71-77.

ATCHLEY, W.R., GASKINS, C.T., & ANDERSON, D. 1976. — Statistical properties of ratios. I. Empirical results. *Syst. Zool.*, **25** : 137-148.

BHAUD, M. 1983. — Comparision of enlarged setae in larvae and adults of *Phyllochaetopterus verrilli* Treadwell (Polychaeta : Chaetopteridae). *Ophelia*, **22** : 257-263.

CHAPMAN, P.M. & BRINKHURST, R.O. 1987. — Hair today, gone tomorrow: induced chaetal changes in tubificid oligochaetes. *Hydrobiologia*, **155** : 45-55.

CONOVER, W.J. 1980. — *Practical nonparametrics*. Second edition. Wiley, New York, 495 pp.

FAUCHALD, K. 1991. — A morphometric study of eunicid polychaetes from Belize, western Caribbean Sea. *Ophelia* Suppl. **5** : 47-53.

FAUCHALD, K. 1992. — A revision of the types of *Palola* (Eunicidae Polychaeta). *J. nat. Hist., Lond.*, **26** : 1177-1227.

GAFFNEY, P.M. 1973. — Setal variation in *Halosydna brevisetosa*, a polynoid polychaete. *Syst. Zool.*, **22** : 171-176.

GARWOOD, P.R. & P.J. OLIVE. 1981. — The significance of the long setal form of *Nephtys caeca* (Polychaeta : Nephtydae) and its relationship to *N. longosetosa*. *Sarsia*, **66** : 195-202.

GRASSLE, J.P. & GRASSLE, J.F. 1976. — Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science*, 192 : 567-569.

GUSTAFSON, G. 1930. — Anatomische Studien über die Polychäten-Familien Amphinomidae und Euphrosynidae. *Zool. Bidrag Uppsala*, **12** : 305-471.

HAND, D.J. 1989. — *Discrimination and classification*. Wiley, New York, 218 pp.

HARTLEY, J. 1984. — Cosmopolitan polychaete species: the status of *Aricidea belgicae* (Fauvel, 1936) and notes on the identity of *A. suecica* Eliason, 1920 (Polychaeta; Paraonidae). *In*: P.A. HUTCHINGS (ed.), *Proc. First International Polychaete Conference*. Linnean Society of New South Wales : 7-20.

HORST, R. 1912. — Polychaeta errantia of the *Siboga*-Expedition. Pt. 1. Amphinomidae. *Siboga-Exped. Monogr.*, **24a** : 1-43.

KRYVI, H. & SORVIG, T. 1990. — Internal organization of limbate polychaete setae (*Sabella pencillus*), with notes on bending stiffness. *Acta Zool.*, **71** : 25-31.

KUDENOV, J.D. 1987. — Review of the primary species characters for the genus *Euphrosine* (Polychaeta: Euphrosinidae). *Bull. biol. Soc. Wash.*, **7** : 184-193.

LEVIN, L.A. 1984. — Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. *Biol. Bull. mar. biol. Lab, Woods Hole*, **166** : 494-508.

MANLY, B. F. J. 1990. — *Multivariate statistical methods: A primer*. Chapman & Hall, London, 159 pp.

MONTGOMERY, D.C. 1984. — *Design and analysis of experiments*. Wiley, New York, 538 pp.

MOORE, J.P. 1905. — New species of polychaetes from the north Pacific, chiefly from Alaskan waters. *Proc. Acad. Nat. Sci. Phila.*, **57** : 525-554.

O'CLAIR, R.M. & CLONEY, R.A. 1974. — Patterns of morphogenesis mediated by dynamic microvilli: chaetogenesis in *Nereis vexillosa*. *Cell Tissue Res.*, **151** : 147-157.

ORRHAGE, L. & P. SUNDBERG. 1990.— Multivariate analysis of morphometric differentiation within the *Laonice cirrata*-group (Polychaeta, Spionidae). *Zool. Scr.*, **19** : 173-178.

Source : MNHN, Paris

ROSS, S. 1988. — *A first course in probability*. 3rd edn MacMillan, 420 pp.

SAS INSTITUTE INC., 1990. — *SAS/STAT user's guide*. Version 6.06, Fourth Edition. North Carolina. 1686 text + 106 pp index.

SCHROEDER, P. 1984. — *Annelida Chaetae*. *In*: BEREITER-HAHN, MATOLTSY & RICHARDS (eds), *Biology of the Integument*. K.S. Springer, New York, **1** : 297-309.

SPECHT, A. 1988. — *Chaete*. *Microfauna Marina*, **4** : 45-59.

SPSS INC., 1990. — *SPSS advanced statistics student guide*. Version 4.0, Chicago, Illinois. 506 pp.

WILLIAMS, S.J. 1984. — The status of *Terebellides stroemi* (Polychaeta; Trichobranchidae) as a cosmopolitan species, based on a worldwide morphological survey, including descriptions of new species. *In*: P. HUTCHINGS (ed.), *Proc. First International Polychaete Conference*. Linnean Society of New South Wales : 118-142.

WILLIG, M.R., OWEN, R.D., COLBERT, R.L. 1986. — Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. *Syst. Zool.*, **35** : 195-203.

Source : MNHN, Paris

# *Pseudonotomastus southerni* gen. nov. sp. nov. a new capitellid from the Celtic Sea

*Lynda M. WARREN* & Miles PARKER***

* Centre for Marine Law and Policy, Cardiff Law School, University of Wales
Cardiff, P O Box 427, Cardiff CF1 1XD, UK
** Department of the Marine, Fisheries Research Centre
Abbotstown, Castlenook, Co. Dublin, Ireland
Present address: Ministry of Agriculture, Fisheries and Food
17 Smith Square, London SW 1P 3JR, UK

ABSTRACT

A new genus and species of Capitellidae has been found in the Celtic Sea off the south coast of Ireland. The genus differs from other genera in having 11 thoracic segments, the first of which is achaetous, the second has capillary chaetae in the notopodia only and the remaining nine have capillary chaetae only. There are no capillary chaetae in the anterior abdominal segments. The type species, *P. southerni*, often shows a distinctive colour pattern.

RÉSUMÉ

***Pseudonotomastus southerni* gen. nov. sp. nov., un nouveau Capitellide en mer Celtique**

Un nouveau genre de Capitellidae a été trouvé en mer Celtique près de la côte sud de l'Irlande. Le genre diffère des autres genres de la famille par la présence de 11 segments thoraciques, dont le premier est achète, le deuxième n'a des soies capillaires que dans les notopodes, et les neuf restant ne possèdent que des soies capillaires. Il n'y a pas de soies capillaires dans les segments antérieurs abdominaux. L'espèce type, *P.southerni*, montre souvent une coloration distincte.

## INTRODUCTION

Specimens of the capitellid described below were collected between 1974 and 1982 in the course of baseline and monitoring surveys off the coast of Cork, Ireland, in the Celtic Sea. They were taken from the vicinity of a disposal site for an industrial organic waste from a fermentation plant. Initially it was thought that the worm could be assigned to the genus *Notomastus*, which also occurs in the area, but, despite strong similarities in gross

WARREN, L.M. & M. PARKER, 1994. — *Pseudonotomastus southerni* gen. nov. sp. nov. a new capitellid from the Celtic Sea. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 299-306. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

morphology, the newly described capitellid can be readily distinguished by its thoracic chaetal formula. The unusual colouration displayed by some specimens (alternating brown and orange bands) is a more obvious, if less reliable, distinction and it was this that first drew our attention to the animal. It is by no means certain, however, that this colour pattern is a natural characteristic of the species. Capitellids usually lose colour in alcohol and appear uniformly pale cream or even colourless although occasionally red pigment spots may persist as, for example, in *Capitella* "punctate" described by HARTMAN (1961) (see WARREN, 1976). The distribution of the coloured bands in this species was reasonably consistent from specimen to specimen but we cannot be certain that it is a natural characteristic. It is possible that the industrial organic waste has resulted in some sort of chemical reaction, perhaps involving gland cells in the epidermis, that has caused a change in colouration. On the other hand, methyl green staining did not reveal any comparable patterns of gland cells either in banded or unbanded specimens.

Specimens were collected by 0.1m$^2$ grabs during a series of surveys extending from 1974 to 1982 (unpublished reports held by the Fisheries Research Centre, Dublin). Samples were fixed in the field using 4 % formalin and later sorted and transferred to 70 % alcohol. Specimens for examination under scanning electron microscopy (SEM) were air dried before coating with gold. Alcohol preserved worms were stained in a 1 % solution of methyl green in 70 % alcohol following Banse (1970).

## ***Pseudonotomastus*** n. gen.

TYPE SPECIES. — *Pseudonotomastus southerni* n. sp.

DIAGNOSIS. — Thorax with 11 segments; peristomium and first segment achaetous; first chaetiger with capillary chaetae in notopodia only; following 9 chaetigers with capillary chaetae only in both rami; abrupt transition between thorax and abdomen.

ETYMOLOGY. — The generic name derives from the superficial resemblance to *Notomastus* Sars, 1850.

## ***Pseudonotomastus southerni*** n. sp.

MATERIAL EXAMINED. — Holotype, incomplete 48 mm long and 26 segments (BM(NH).ZB.1982.89), and 33 paratypes [BM(NH).ZB.1982.90-122] in 18 samples, all incomplete and including several abdominal fragments. Three paratypes were prepared for SEM. These specimens have been deposited in the British Museum (Natural History) as part of a collection of Irish polychaetes by the second author in 1983.

TYPE LOCALITY. — Celtic Sea, off Cork, Ireland. The holotype was collected at 8°20' W, 51°30' N; the remaining specimens in an area between 7°50' to 8°26' W, and 51°27' to 51°42' N.

ETYMOLOGY. — Named after Rowland SOUTHERN (1882-1935), sometime naturalist with the Fisheries Branch of the Department of Agriculture and Technical Instruction, the original antecedent of today's Fisheries Research Centre of the Irish Department of the Marine (GREENE, 1936). Southern wrote many papers on the annelids of Ireland, including one on the annelids of Dublin Bay (SOUTHERN, 1910) and the archiannelid and polychaete section of the Clare Ireland Survey (SOUTHERN, 1914). These were among the first, and remain among the most important, systematic analyses of the Irish polychaetes.

MORPHOLOGY. — The species has a robust appearance. No complete specimen has been recorded but it is estimated from the size and shape of the material available that the total length might be more than 150 mm. The body is divided into a muscular thorax with no clear parapodial ridges followed by a slightly thinner, tapering abdomen in which there are distinct parapodial ridges (Fig. 1c). The length of the thorax is about 8 to 10 mm and the width about 1.2 mm. There are distinct grooves running along the length of the abdomen in a dorso-lateral position in the space between the notopodia and neuropodia and less clear lateral and ventral grooves (Fig. 1a).

The prostomium is triangular in outline with a concave surface ventrally. It is surmounted by a prominent palpode (Fig. 1d). In some specimens the peristomium is drawn forward over the prostomium like a hood so that only the palpode is visible (Fig. 1c). Large nuchal organs were apparent in one specimen but were otherwise indistinct. Eyes were not detected.

Source : MNHN, Paris

The peristomium is a distinct ring about as wide as the following segments and considerably more prominent than the prostomium. There is a large eversible proboscis which is heavily papillated (Fig. 1d) although in some specimens the papillae are not easily visible because of proboscis has become flaccid in preservation.

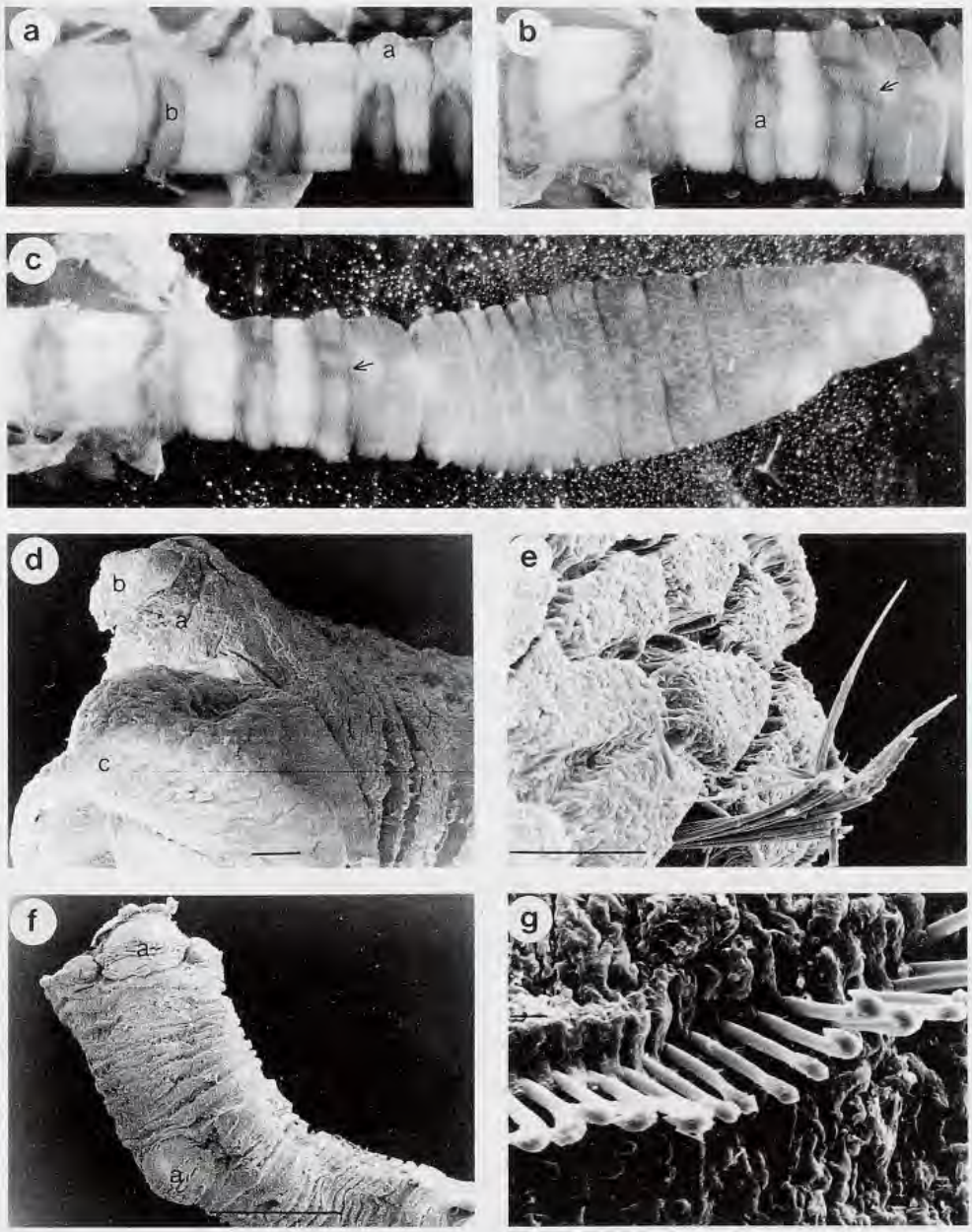



FIG. 1. — *Pseudonotomastus southerni* n. sp. a, anterior abdominal segments, dorsal view (a, notopodium, b, neuropodium). b, anterior abdominal segments, ventral view (arrow indicates boundary between thorax and abdomen, a - neuropodium). c, thorax and anterior abdomen (arrow indicates boundary between thorax and abdomen). d, prostomium and everted proboscis (SEM) (a, prostomium, b, palpode, c, proboscis, scale bar = 100 µm). e, thorax, showing reticulation and capillary chaetae (SEM) (scale bar = 100 µm). f, abdominal segments (SEM) (a - notopodia, scale bar = 1 mm). g, abdominal neuropodial hooks (SEM) (scale bar = 10 µm).

The thorax consists of 11 segments and can be divided into two regions separated by a transitional zone. Segments 1-4 are wide with few constrictions either between segments or on them so that the overall impression

Source : MNHN, Paris

is of a smooth rounded outline. The surface is, however, heavily reticulated (Fig. 1e). Segments 7-11 are slightly narrower. There are usually deep constrictions between segments and each segment is divided into two equal halves by a deep annulus. The outline is thus somewhat angular and truncated. The surface is smooth with only slight reticulations in some specimens. Segments 5 and 6 are transitional, the degree of reticulation and constriction varying from one specimen to another. There are no parapodial lobes or ridges on any thoracic segments.

The division between thorax and abdomen is very distinct (Figs 1b-c). Abdominal segments are about one and a half times as long as thoracic segments in the anterior region and become progressively longer further back. The parapodia are present as prominent ridges in the case of the neuropodia and a fleshy pad in the case of the notopodia (Figs 1a,b,f). The neuropodia almost meet mid-ventrally and extend around the sides of the worm terminating in a fleshy cirrus, which may have a branchial function, on the dorsal surface (Fig. 2). The notopodial pads coalesce so that in most specimens a single pad is visible situated mid-dorsally between the neuropodia (Figs 1a, 1f, 2). The lateral margins of the notopodia are drawn out into small cirri. In one specimen pores, presumably nephridial, are prominent immediately posterior to these cirri in all abdominal segments present (i.e. fifteen). We do not know why these pores are not obvious in other specimens but suggest that the differences may reflect sexual condition.

Several of the specimens show an unusual pattern of colour banding (Figs 1a-b). The basic colour in alcohol is pale creamy yellow. The pattern is most obvious on the abdomen where there are brown/orange bands around the neuropodial ridges sometimes extending into the immediate vicinity of the chaetae and always extending for a small way either side of the neuropodium. Dorsally the band usually stops at the neuropodial cirri but there is occasional light staining on the notopodial pad. In the thorax the pattern is much more variable but is usually darker on segments 7-11 and is often absent from the peristomium. The prostomium is never coloured. On the thorax the colour only occurs on the flat surfaces, i.e. the tops of the reticulations and the main body of the hind thorax. There is no colouration in the cracks and deep annuli. Under high power light microscopy the colouration appears as dark orange irregularly shaped and sized granules in the epidermis. It must be noted that this colour pattern is not present in all animals. Its presence could not be correlated with size or sexual condition. It is possible that the pattern is an artifact caused by differential staining by something in the sediment. Staining the worms with methyl green produced no obvious staining pattern. Colour was taken up evenly by the worms but was lost most rapidly from the prostomium and everted proboscis.

There are 10 thoracic chaetigers, all with capillary chaetae only. These are arranged in four bundles with the neurochaetae situated ventro-laterally and the notochaetae much closer together mid-dorsally. The first segment after the peristomium is achaetous. This is followed by a segment with notochaetae only. The remaining 9 segments have both noto- and neurochaetae thus giving the thoracic chaetal formula of 1 -, $2^{c}$, 3-11C. The number and size of the capillaries increases posteriorly. On segments 2 and 3 they can be difficult to see and there are usually only 4 or 5 per bundle. By segment 11 there may be over 20 per bundle (Fig. 1e). In most cases the bundles on segments 7-11 are prominent whereas the anterior ones are less readily detected. The chaetae have a delicate, feather-like appearance under light microscopy and are only slightly tapered with no wings. This structure is confirmed under SEM.

Hooded hooks are the only type of chaetae found on the abdomen but, as no complete specimens have been examined, it is possible that other types may occur. The notopodial hooks are borne in bundles of between 30 and 36 in the first few abdominal segments, decreasing to about 25 hooks by abdominal segment 10. On the abdominal neuropodia hooded hooks are borne in a single row extending from the ventral surface around onto the dorsal surface of the worm and number in excess of 40 (Fig. 1g). There was little individual variation in chaetal numbers.

Both notopodial and neuropodial abdominal chaetae are small short-handled hooded hooks protruding only a short way from the body of the worm. The hoods are prominent and tight fitting, extending from about half way up the shaft and enveloping the main fang of the hook so that only the tip is visible. The main fang is long and pointed (Fig. 1g) and is surmounted by numerous equally-sized minute teeth that give the impression of a ridge.

None of the specimens is complete. The longest specimen exceeds 110 mm but most are no more than 40 mm. There are at least 26 abdominal segments.

ECOLOGY. — Little is known about the ecology of this species. The area from which these specimens were taken lies some 20 to 30 km south of the entrance to Cork Harbour, in 70-90 m depth of water. The area is characterised by mixed poorly sorted sediments, slightly coarser at shallower sites closer to shore and muddier offshore. Faunal density is generally low, of an "*Amphiura filiformis*" type assemblage (THORSON, 1957), with dominant polychaete species including *Lumbrineris gracilis*, *Spiophanes kroyeri* and *Owenia fusiformis*.

Source : MNHN, Paris

The centre of the collection area has been used since 1975 for the disposal of organic waste from a fermentation plant in Cork, but there were no obvious signs of organic enrichment in the sediment, or site-related perturbations in the faunal distribution. The samples collected in 1974 in any case pre-date the disposal operation.

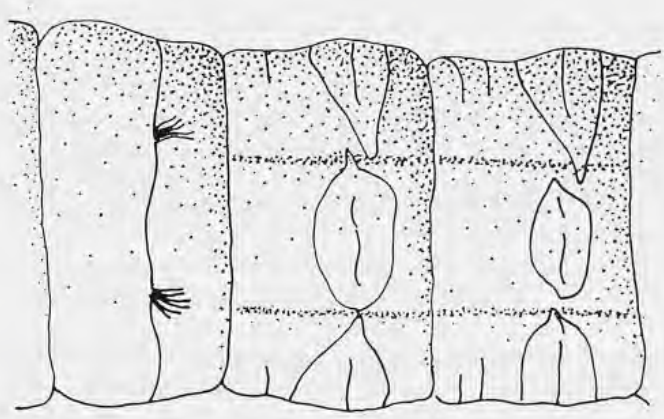


FIG. 2. — Dorsal view of last thoracic and first two abdominal segments. Width of first abdominal segment is 1.5 mm.

There are no obvious differences to distinguish sex. One abdominal fragment, presumed to belong to this species, contains small, rounded eggs.

## DISCUSSION

The diagnosis of new genera, and even species, of capitellids is often not completely satisfactory because there are few suitable morphological characteristics and too few specimens to determine variations within a species.

We believe that the most reliable generic character is the number of thoracic chaetigers especially where, as in this case, the distinction between thorax and abdomen is clear. It should be noted, however, that there has been considerable confusion as to the number of achaetous segments at the front end of a capitellid (see WARREN, 1991). Sometimes the peristomium is regarded as pre-segmental; in other cases it is counted as an achaetous segment. On some occasions it has been referred to in both ways within a single paper. Often, also, figures illustrating species characteristics do not accord with the written description (see, for example, KIRKEGAARD, 1983 in which the description of *Paracapitella* refers to the peristomium as an achaetous segment but the drawing appears to indicate a peristomium and an achaetous first segment).

The number of thoracic chaetigers alone will not suffice to distinguish all genera and it is necessary to resort to characteristics of the chaetae and their distribution. This must be done with caution, however, as chaetal distributions, especially in the posterior thorax, change with age.

The overall body shape and the relative prominence of the prostomium and, if present, the palpode are known to be affected by fixation so that these characteristics are not reliable for diagnosis. It is worth noting, however, that the blunt-ended appearance in some specimens of *Pseudonotomastus*, caused by the peristomium being drawn forward like a hood, is reminiscent of *Notomastus* and unlike the appearance of other capitellids such as *Capitella* where the fusion of the peristomium prevents it from being drawn forward.

References to long- or short- handled hooded hooks occur in most descriptions of capitellid species. We describe those of *Pseudonotomastus* as being short-handled but we concede that this is a subjective observation and further note that the character might be affected by fixation. The detailed structure of the hook is of greater potential value for diagnosis although not usually for identification purposes because differences are only apparent under high magnification. The numbers of teeth above the main fang in *Pseudonotomastus* are too great for easy counting and we concluded that precise number counts could not be obtained with any degree of accuracy. Of greater importance

Source : MNHN, Paris

than the numbers of the teeth may be the fact that all the teeth are the same size unlike the case with some capitellid species where the central tooth is larger than the rest.

Because no complete specimens have been examined we cannot be certain that hooded hooks are the only chaetae on the abdomen. It is not uncommon among capitellids for there to be different types of chaetae on posterior abdominal segments.

One of the most distinctive features of some of the specimens of *P. southerni* is the colour banding. Pigmentation is not unknown in capitellids and has, for example, been recorded in *Capitellethus dispar* Thomassin, 1970 where the last thoracic and first abdominal chaetigers are patterned with brown rings made up of small pigment spots. We think, however, that the diagnostic significance of this feature will only become apparent when further populations of *Pseudonotomastus* are found and examined. The lack of any staining pattern with methyl green, however, contrasts with results obtained from an extensive range of museum material belonging to *Notomastus* which produced a staining pattern that highlighted the parapodial ridges. It is possible that this feature could be of use in sorting material of the two genera.

We conclude that the distinctive features of the genus *Pseudonotomastus* are that it has 11 thoracic segments, with 10 thoracic chaetigers on the first of which chaetae are restricted to the notopodia. All thoracic chaetae are simple capillary chaetae.

Five genera of capitellids with 10 thoracic chaetigers have been described. Three of these (i.e. *Mediomastus* Hartman, 1944, *Parheteromastides* Hartmann-Schröder, 1962 and *Neomediomastus* Hartman, 1969) may be readily distinguished from *Pseudonotomastus* by the presence of hooded hooks in the thorax. *Neonotomastus* Fauchald, 1972 and *Pseudoleiocapitella* Harmelin, 1964 both have an achaetous first segment followed by 10 thoracic chaetigers with capillary chaetae. In *Neonotomastus* the first thoracic chaetiger has capillary chaetae in the notopodia only whereas *Pseudoleiocapitella* has the first chaetiger complete. These genera may be distinguished from *Pseudonotomastus* by the presence of capillary chaetae in the first two abdominal segments.

*Decamastus* Hartman, 1963 is most like *Pseudonotomastus* in its chaetal formula but lacks the first achaetous thoracic segment. The type species, *D. gracilis*, has a full complement of capillary chaetae on all 10 thoracic chaetigers but *D. nudus* Thomassin, 1970 is distinguished by the absence of neuropodial chaetae on the first chaetiger.

*Capitellethus* Chamberlin, 1919, as typified by *C. dispar* (EHLERS, 1907) may be distinguished from *Pseudonotomastus* by the presence of 11 chaetigers with capillary chaetae, of which the first has only notopodial chaetae. There is no mention of an achaetous segment and it is possible that some confusion of segment counts might have occurred. (This certainly happened in FAUCHALD (1977) which lists *Capitellethus* as having 10 thoracic chaetigers). Apart from the different number of thoracic chaetigers, *Capitellethus* differs from *Pseudonotomastus* in having an indistinct boundary between the thorax and the abdomen and in having long hooks on the abdomen.

Despite similarities between *Pseudonotomastus* and both *Decamastus* and *Capitellethus*, the new genus is most like *Notomastus* Sars, 1850 and strongly resembles it in gross morphology, including the arrangement of the parapodial ridges and the shape of the thorax. *Pseudonotomastus* can be distinguished from *Notomastus* only by the presence of an extra thoracic chaetiger in *Notomastus*.

It is, perhaps, unwise to speculate on the affinities of this genus on the basis of so few data but the similarity with *Notomastus* is so striking as to merit comment. The specimens of *Pseudonotomastus* were collected with *Notomastus latericeus* Sars, sometimes in the same sample. *Notomastus* is a very large genus, subdivided by some into sub-genera.

The description of this new species as typical of a new genus raises some questions concerning diagnostic characters in capitellids. The number of thoracic chaetigers is one of the few reliable diagnostic features of capitellids and its usefulness presumably reflects genotypic characteristics that are susceptible to change. Some species have chaetae in both rami of all thoracic chaetigers; in others the first chaetiger has notopodial chaetae only. Similarly, *Decamastus nudus* is placed in the same genus as *D. gracilis* even though it lacks chaetae in the neuropodia of the first chaetiger. In this paper, the presence of a first chaetiger with chaetae restricted to the notopodia is regarded as being of generic significance. We made this decision for the following reasons. Intraspecific variation in the distribution of chaetae on the anterior thorax is unusual. Given our knowledge of the development of capitellids (see, for example, WILSON, 1933; RASMUSSEN, 1956) this is not surprising. The presence or absence of notopodia on the first chaetiger is, therefore, likely to be of significance. Until now this feature has been used both as a specific and a generic distinction without further explanation. In the absence of the detailed information necessary to reach a definitive decision on this point, we think that it is in order to use the feature as a generic character in order to prevent confusion. We accept that further knowledge may refute our

Source : MNHN, Paris

diagnosis and, indeed, we hope that by raising this issue here we may stimulate a thorough review of this feature in capitellids.

## ACKNOWLEDGEMENTS

We are indebted to the Polychaete section of the British Museum (Natural History) and to the National Museum of Wales for providing research facilities and to the staff at the Electron Microscope Unit of the University of London Goldsmiths' College for technical assistance. We gratefully acknowledge the assistance of B.A. THOMAS in preparing the illustrations. M. PARKER gratefully acknowledges the assistance of the Fisheries Research Centre and access to unpublished information. We are also indebted to Ivor REES of the University College of North Wales who provided samples from the 1974 survey.

## REFERENCES

BANSE, K., 1970. — The small species of *Euchone* Malmgren (Sabellidae, Polychaeta). *Proc. biol. Soc. Wash.*, **83** : 387-408.

CHAMBERLIN, R.V., 1919. — The annelida polychaeta. *Mus. Comp. Zool. Harvard, Mem.*, **48** : 1-514.

EHLERS, E., 1907. — Neuseeländischen Anneliden II. *Abh. K. Ges. wiss. Göttingen, Math.-Phys. Kl. n.F.*, **3** : 1-80.

FAUCHALD, K., 1972. — Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. *Allan Hancock Monogr. mar. biol.*, **7** : 1-575.

FAUCHALD, K., 1977. — The polychaete worms. *Natural History Museum of Los Angeles County, Science Series*, **28** : 1-190.

GREENE, A.C., 1936. — Rowland Southern, Obituary. *J. Cons. Perm. Int. Explor. Mer.*, **11** : 3-6.

HARMELIN, J.G., 1964. — Étude de l'endofaune des mattes d'herbières de *Posidonia oceanica* Delib. *Rec. Trav. Stn. Mar. Endoume*, **51** : 43-105.

HARTMAN, O., 1944. — Polychaetous annelids from California, including the descriptions of two new genera and nine new species. *Allan Hancock Pacif. Exped.*, **10** : 239-310.

HARTMAN, O., 1961. — Polychaetous annelids from California. *Allan Hancock Pacif. Exped.*, **25** : 1-226.

HARTMAN, O., 1963. — Submarine canyons of Southern California Pt. III. Systematics: Polychaetes. *Allan Hancock Pacif. Exped.*, **27** : 1-93.

HARTMAN, O., 1969. — *Atlas of the Sedentariate Polychaetous Annelids from California.* Allan Hancock Foundation, California, 812 pp.

HARTMANN-SCHRÖDER, G., 1962. — Zweiter Beitrag zur Polychaetenfauna von Peru. *Kieler Meeresforsch*, **18** : 109-147.

KIRKEGAARD, J.B., 1983. — Bathyal benthic polychaetes from the north east Atlantic Ocean, south west of the British Isles. *J. mar. biol. Ass. UK*, **63** : 593-608.

RASMUSSEN, E., 1956. — The reproduction and larval development of some polychaetes from the Isefjord, with some faunistic notes. *Biol. Meddr.*, **23** : 1-84.

SARS, M., 1850. — Beretning om en i Sommeren 1849 foretagen zoologisk Reise i Lofoten og Finmarken. *Nyt Mag. Naturvid*, **6** : 121-211.

SOUTHERN, R., 1910. — The marine worms (Annelida) of Dublin Bay and the adjoining district. *Proc. R. Irish Acad.*, XXVIII, B, **6** : 215-246.

SOUTHERN, R., 1914. — Clare Island Survey, Part 47, Archiannelida and Polychaeta. *Proc. R. Irish Acad.*, XXXI, **47** : 1-160.

THOMASSIN, B., 1970. — Contribution à l'étude des polychètes de la région de Tulear (S. W. de Madagascar). III. Sur les Capitellidae des sables coralliens. *Rec. Trav. Stn mar. Endoume* suppl., **10** : 71-101.

Source : MNHN, Paris

THORSON, G., 1957. — Bottom communities (sublittoral or shallowshelf). *In*: J.W. HEDGPETH (ed.), *Treatise on Marine Ecology and Palaeoecology, vol 1, Ecology*. Geological Society of America : 461-534.

WARREN, L.M., 1976. — A review of the genus *Capitella* (Polychaeta, Capitellidae). *J. Zool., Lond.*, **180** : 195-209.

WARREN, L.M., 1991. — Problems in capitellid taxonomy. The genera *Capitella*, *Capitomastus* and *Capitellides* (Polychaeta). *Ophelia* suppl., **5** : 275-282.

WILSON, D.P., 1933. — The larval stages of *Notomastus latericeus* Sars. *J. mar. biol. Ass. UK*, **18** : 511-518.

Source : MNHN, Paris

# A new species of *Chaetozone* (Polychaeta, Cirratulidae) from Europe, with a re-description of *Caulleriella zetlandica* (McIntosh)

*Annette WOODHAM* & Susan CHAMBERS***

* Environment and Resource Technology Ltd
Old St. James Church, Port Edgar, South Queensferry, EH30 9SQ, U.K.
** National Museums of Scotland
Chambers Street, Edinburgh, EH1 1JF, U.K.

ABSTRACT

*Chaetozone setosa* Malmgren, 1867 is common in soft sediments from the intertidal zone to the deep sea and is recorded as having a cosmopolitan distribution. It has been apparent for some time that more species of *Chaetozone* may be present than are currently recognised. During benthic monitoring in the English Channel, a distinct species of *Chaetozone*, *C. gibber* sp. nov. was recognised. The new species is described in detail and distinguished from *C. setosa*. As *Caulleriella zetlandica* (McIntosh, 1911) is similar in overall appearance and lacks a full description, this species is re-described from material obtained near the type locality. Although the spines of both species are unidentate in fully grown individuals, *C. zetlandica* can be distinguished from *C. gibber* by the lack of spines in the notopodia. The need for re-definitions of the genera *Chaetozone* and *Caulleriella* is discussed.

RÉSUMÉ

**Une nouvelle espèce de *Chaetozone* (Polychètes, Cirratulidae) en Europe, avec une redescription de *Caulleriella zetlandica* (McIntosh)**

*Chaetozone setosa* Malmgren, 1867 est une espèce commune dans les sédiments meubles, depuis la zone intertidale jusqu'aux grandes profondeurs et présente une distribution cosmopolite. Depuis quelques temps, il s'est avéré qu'il existait davantage d'espèces de *Chaetozone* qu'on ne l'admettait habituellement. Au cours d'un suivi des peuplements benthiques de la Manche, une espèce distincte de *Chaetozone*, *C. gibber* sp. nov. a été reconnue. La nouvelle espèce est décrite en détail et comparée à *C. setosa*. *Caulleriella zetlandica* (McIntosh, 1911), espèce d'aspect général similaire et dont on ne possédait pas de description complète, est redécrite d'après des spécimens obtenus près de la localité type. Quoique les épines des deux espèces soient unidentées chez les individus adultes, *C. zetlandica* peut être distinguée de *C. gibber* par l'absence d'épines au notopode. Le besoin d'une redéfinition des genres *Chaetozone* et *Caulleriella* est commenté.

---

WOODHAM, A. & S. CHAMBERS, 1994. — A new species of *Chaetozone* (Polychaeta, Cirratulidae) from Europe, with a re-description of *Caulleriella zetlandica* (McIntosh). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 307-316. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

*Chaetozone setosa* Malmgren, 1867 has been recorded from the intertidal zone to the deep sea, and from such widespread areas as the Arctic (MALMGREN, 1867), north Pacific (HARTMAN, 1961) and West Africa (DAY, 1967). It is the only species of *Chaetozone* recorded from the eastern North Atlantic area (SOUTHERN, 1914; FAUVEL, 1927; HARTMANN-SCHRÖDER, 1971; HOWSON *et al*, 1987), although its apparent variability in form has been noted (CHRISTIE, 1985; LECHAPT, 1983; pers. obs.).

During benthic monitoring in the English Channel, an undescribed bi-tentaculate cirratulid was discovered. It possesses spines with unidentate tips only and, following the definitions of HARTMAN (1961), is assigned to *Chaetozone*. The new species is most similar in appearance to *Caulleriella zetlandica* (McIntosh, 1911), a species common around the British Isles but originally described from a posterior fragment only. This species is re-described using abundant material collected during surveys close to the type locality in Shetland. A syntype of *Caulleriella caputesocis* (de Saint-Joseph, 1894), another species distinguished by spines with unidentate tips and recorded from European waters, was also re-examined.

## MATERIALS AND METHODS

The bulk of the specimens of *Chaetozone gibber* sp. nov. and *Caulleriella zetlandica* were collected using a van Veen grab during benthic monitoring surveys off Folkestone, Kent, U.K. and in Sullom Voe, Shetland, U.K. respectively. Samples were sieved through a 1.0 mm (*C. gibber* sp. nov.) or 0.5 mm (*C. zetlandica*) mesh and the retained material fixed in an approximately 10 % formalin solution, later being transferred to a 2 % phenoxytol solution containing Rose Bengal stain to aid sorting. Material for scanning electron microscopy (SEM) was relaxed for two hours in magnesium chloride solution before fixation. After washing in distilled water, it was dehydrated through an acetone series, critical point dried and gold-coated. Specimens were examined using a Wild M7 stereomicroscope and a Cam Scan Series 4 SEM. All drawings were prepared with the aid of a camera lucida.

Additional material from the National Museum of Wales (NMW), National Museum of Ireland (NMI), British Museum (Natural History) (BMNH), Muséum National d'Histoire Naturelle (MNHN) and the Plymouth Marine Laboratory (PML) was also examined.

## SYSTEMATICS

### *Chaetozone gibber* sp. nov.

MATERIAL EXAMINED. — U.K.: off Folkestone, Kent, SE England, very fine silt-medium sand, 3.5-20.5 m, numerous specimens collected by Environment and Resource Technology Ltd (ERT) and deposited in the National Museums of Scotland, NMSZ 1992.89; Turnaware Point, Cornwall, SW England, 4.3 m, two specimens, NMWZ 1992.046.5; Milford Haven, S Wales, 46 specimens, NMWZ 1985.083 and .087. France: Banyuls-sur-Mer, 40-45 m, two specimens, NMWZ 1992.03.

TYPE MATERIAL. — One holotype and nine paratypes from Folkestone are deposited in the National Museums of Scotland (Holotype NMSZ 1992.87, Paratypes NMSZ 1992.88). The holotype measures 19 mm for 115 chaetigers. Paratype material is also deposited in the British Museum (Natural History) (BMNH 1992.427-432), the National Museum of Wales (NMWZ 1993.009) and the Muséum National d'Histoire Naturelle (MNHN 1992 U.C.355).

DESCRIPTION. — Length of body up to 20 mm for approximately 200 segments. Body surfaces smooth; dorsal surface swollen anteriorly between chaetigers 7-30 approximately, giving a characteristic hump-backed appearance (Figs 1c & 3a); ventral surface flattened with a longitudinal groove; posterior region bluntly tapered, dorso-ventrally compressed with lateral surfaces somewhat flattened giving almost rectangular shape in cross section (Fig. 1e). Segments broad, short and crowded in anterior region, becoming narrower and longer posteriorly, without intersegmental constrictions. Colour of preserved material (in alcohol) creamy white.

Prostomium conical with acutely pointed tip. Pair of subdermal eyes, round to elongate, near lateral posterior margins; shallow nuchal groove below and behind each eye (Fig. 1c).

Source : MNHN, Paris

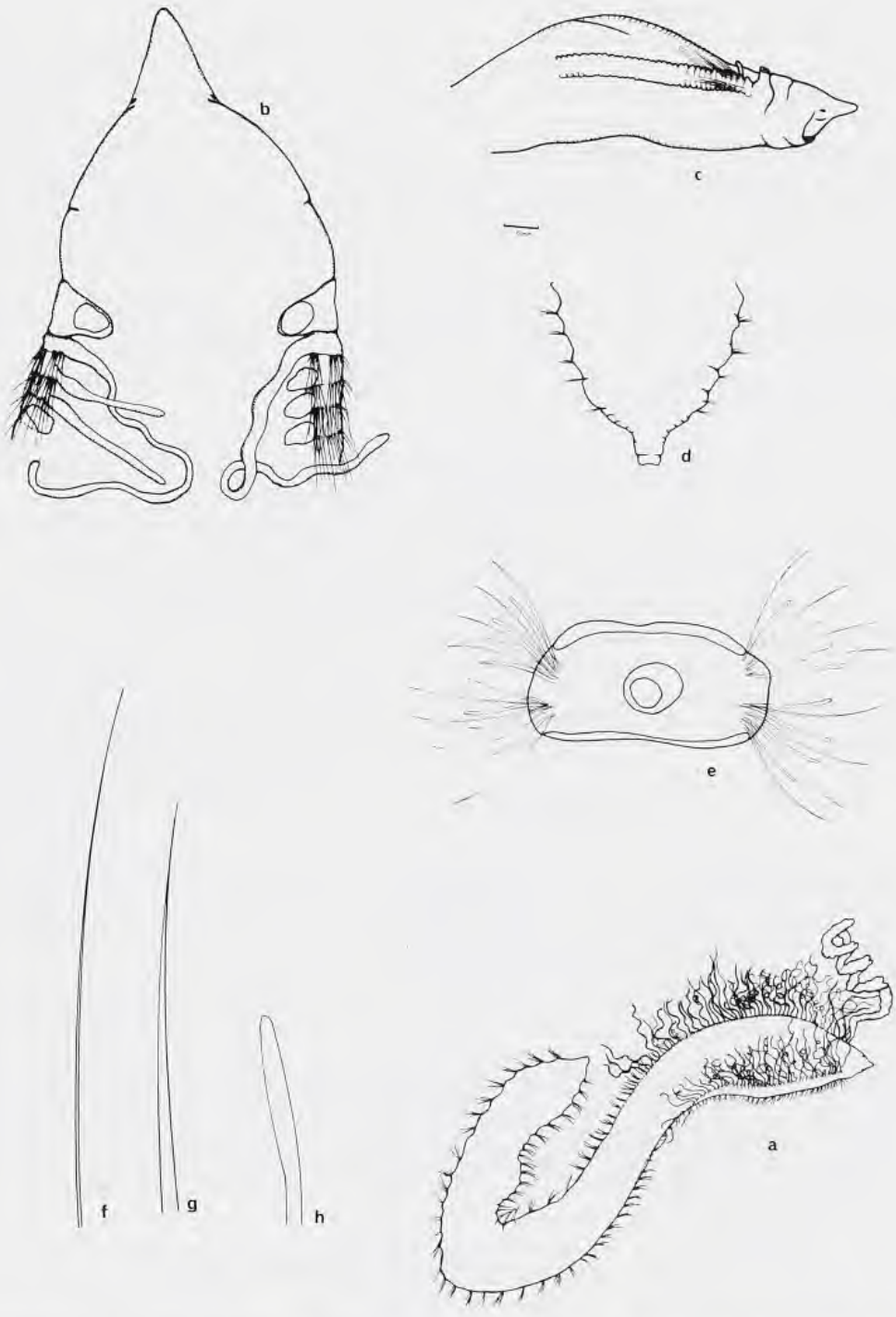



FIG. 1. — *Chaetozone gibber* sp. nov. from Folkestone: **a**, complete animal, holotype. **b**, anterior end, dorsal view. **c**, anterior end, lateral view. **d**, posterior region, dorsal view. **e**, cross section of posterior segment. **f**, slender capillary chaeta. **g**, stout awl-shaped capillary chaeta from mid-body notopodium. **h**, spine with blunt unidentate tip from posterior chaetiger.

Source : MNHN, Paris

Peristomium achaetous, smooth, partially divided into 3 annuli, pair of grooved tentacular palps originating from dorsal surface of posterior annulus, measuring approximately 1/3 of body length. First pair of branchiae arising immediately posterior to tentacular palps, on first chaetiger (Fig. 1b). Mouth ventral (Fig. 1c).

Parapodia all biramous with notochaetae and neurochaetae; parapodial lobes flattened mounds, extending further from the body posteriorly. Pair of branchiae arising dorsal to notopodial lobes (Figs 1b,c & 3b) on every chaetiger in anterior region, occurring less regularly in mid-body region and absent posteriorly (precise occurrence of branchiae uncertain as frequently only scars remain in preserved specimens); branchial filaments simple, cylindrical and smooth, of variable length up to approximately 2 mm, thickest and longest in anterior region.

Notopodia and neuropodia slightly separated with chaetae arranged in single dorsal-ventral rows (Fig. 1e). Chaetae directed laterally in anterior and mid-body regions and more anteriorly in posterior third of body. Chaetae of three types: i) slender capillaries (Fig. 1f) in both rami of all chaetigers; ii) stout awl-shaped capillaries (Figs. 1g and 3d) in notopodia between approximately segments 40 and 90; iii) spines with unidentate tips (Figs. 1h and 3c) in notopodia from mid-body (segments 90-100) to end of body and in neuropodia from anterior region (segments 50-80) to end of body; number of spines in each ramus increasing posteriorly from 1 to 4; each ramus in posterior region of body typically with four unidentate spines and four slender capillaries alternating with each other (Fig. 1e); left and right chaetal rows well-separated, spines not forming complete rings around segments.

Pygidium with small ventral lobe (Fig. 1d).

REMARKS. — *Chaetozone gibber* can be readily recognised by its characteristic shape (a dorsal hump anteriorly and a tapering, dorso-ventrally flattened posterior end) and by its distinct eyes.

Nine complete specimens of *Chaetozone setosa* Malmgren, 1867 from Spitzbergen, collected by M. Kendall (PML) have been examined. The largest specimen measures 14 mm for 80 segments. The diagnostic characters of complete rings of spines and intersegmental constrictions giving a concertina-like appearance to the posterior third of the body, extremely long capillary chaetae in the middle third of body, and absence of eyes agree well with Malmgren's description and figures. A full re-description of *C. setosa* is required in order to provide a basis for the re-examination of eyeless *Chaetozone* in northern European waters; this is outside the scope of the present paper. *C. gibber* is distinguished from *C. setosa* by the presence of eyes and the anterior dorsal hump, and by the flattened shape of the posterior region with its lack of both "concertina" segments and complete rings of spines.

Eight specimens collected by J-P. LECHAPT from the Rance estuary and labelled Cirratulidae sp. A have been examined. Although these resemble *C. gibber* very closely, LECHAPT (pers. comm.) has found plumose chaetae in his material and these have not been observed by us in the *C. gibber* material from Folkestone and other localities.

*Chaetozone gibber* is most similar in overall appearance to *Caulleriella zetlandica* (McIntosh, 1911): both species possess a distinct pair of eyes and a broader anterior region with flattened, tapering posterior end. It can be separated from *C. zetlandica* by the presence of a distinct dorsal hump, and of blunt unidentate spines in both rami, rather than in the neuropodium only. *Caulleriella zetlandica* also possesses bidentate spines in small individuals; an examination of a wide range of sizes has failed to reveal these in *C.gibber*.

In European waters, *Caulleriella caputesocis* (de Saint-Joseph, 1894) is the only other bi-tentaculate cirratulid reported to have eyes and to possess unidentate spines in both rami. As the precise identity of this species is unclear, and the original figures uninformative, a syntype of *Heterocirrus caputesocis* (MNHN A181) was examined. It is in poor condition and in three pieces, measuring 15 mm for 75 segments in total. The eyes figured and described by Saint-Joseph are not visible. The specimen does not closely resemble the original figures, but unidentate spines are present in the posterior region and these do not form complete rings around the body. The overall shape of the body and of the head clearly separates *C.gibber* from this specimen, which cannot be assigned to any known species from the UK.

ETYMOLOGY. — The specific name *gibber* is the Latin word meaning hump-backed.

DISTRIBUTION AND HABITAT. — The species has been recorded from the south coasts of England and Wales and the Mediterranean coast of France, from depths of 3.5-45 m. It has been found in silty and sandy sediments and in abundances of up to 245 ind. $m^{-2}$. The benthic fauna at Folkestone, England, U.K. (type locality) has been monitored annually since 1983 and is very similar to the *Abra alba-Melinna palmata* community described by IBANEZ & DAUVIN (1988) from the Bay of Morlaix area of the western English Channel (Institute of Offshore Engineering/ERT, unpublished reports). *Chaetozone gibber* sp. nov. has appeared constantly in samples collected each year throughout this period. A species identified as *C. setosa* is present in the same community.

Source : MNHN, Paris

## Re-description of *Caulleriella zetlandica* (McIntosh, 1911)

*Chaetozone zetlandica* McIntosh, 1911: 161 (type locality: St. Magnus Bay, Shetland, U.K). — SOUTHERN, 1914: 115, pls 12 and 13, Figs 29 A-K
*Heterocirrus zetlandica.* — FAUVEL, 1927: 99, Figs 34 i-n
*Caulleriella zetlandica.* — DAY, 1976: 507

MATERIAL EXAMINED. — U.K.: Holotype of *Chaetozone zetlandica,* St. Magnus Bay, Shetland, Scotland, 100 fathoms (≈ 170 m), posterior fragment in two pieces, BMNH 1921.5.1.3232; Sullom Voe, Shetland, Scotland, very fine to medium sand, 17-31 m, numerous specimens collected by ERT April 1991 and April 1992, identified as *Caulleriella zetlandica,* NMSZ 1992.89. Ireland: Fahy Bay, Clare Island, six specimens collected by Southern and assigned by him to *Chaetozone zetlandica* "stage A", NMI 77.1908.

DESCRIPTION. — The following description is based on the recently-collected material from Shetland. This material is abundant, in good condition and includes whole specimens of a wide range of sizes. For consideration of other material (including the holotype), see *Remarks*.

Length of body up to 24 mm for approximately 154 segments. Body surfaces smooth, slightly irridescent. Dorsal surface of anterior half of body rounded, becoming flatter posteriorly; ventral surface flattened with longitudinal groove; posterior region bluntly tapered, dorso-ventrally compressed to give an oval shape in cross section (Fig. 2b). Segments of relatively even length, without intersegmental constrictions.

Prostomium conical with long, acutely pointed tip. Pair of subdermal eyes, round to elongate, near lateral posterior margin; shallow nuchal groove posterior to each eye (Fig. 2a).

Peristomium achaetous, smooth, partially divided into three annuli, pair of tentacular palps originating from dorsal surface of posterior annulus (only stumps present on all specimens). First pair of branchiae originate immediately posterior to tentacular palps, on first chaetiger. Mouth ventral (Figs 2a & 4a).

Parapodia all biramous with neurochaetae and notochaetae; parapodial lobes flattened mounds, extending further from body posteriorly. Pair of branchiae arising dorsal to notopodial lobes (Figs 2a & 4a) and occurring on every chaetiger in anterior region then irregularly in mid-body and posterior regions (precise occurrence of branchiae uncertain as frequently only scars remain in preserved specimens); branchial filaments simple, smooth, of variable length up to approximately 4 mm.

Notopodia and neuropodia slightly separated, with chaetae arranged in single dorsal-ventral rows, directed latero-posteriorly in anterior and mid-body regions and more anteriorly in posterior third of body. Chaetae of 5 types: i) slender capillaries (Fig. 2c) in notopodia only in all chaetigers; ii) stout awl-shaped capillaries of medium length (Fig. 2d), occurring in both rami of all chaetigers; iii) short stout awl-shaped capillaries (Fig. 2e), in mid-body neuropodia only; iv) spines with unidentate tips (Figs 2f & 4c) in neuropodia of posterior region; v) spines with bidentate tips (e.g. Figs 2g & 4d) in neuropodia of juvenile or small specimens only. Spines with bidentate tips found in individuals 4-5 mm long, although those in dorsal position of same neuropodia approach unidentate forms (Fig. 4c). All spines in larger individuals with unidentate tips only.

Pygidium with small ventral button-like lobe.

REMARKS. — *Chaetozone zetlandica* McIntosh, 1911 was described from a single headless fragment dredged from St Magnus Bay, Shetland. Examination of the holotype has shown it to be in very poor condition and in two parts, the anterior section measuring 15 mm by 1 mm for 46 chaetigers and the posterior section including the pygidium 1 mm by less than 1 mm for 7 chaetigers. Most of the chaetae are broken, but are clearly in well-separated rows; not forming complete rings around the body in the posterior segments. Both capillary and acicular chaetae (spines) are present but, due to the poor condition, it is difficult to interpret dorsal and ventral surfaces of the body. Tips of all complete spines are unidentate. No bidentate tips were seen. MCINTOSH separated his specimen from *Chaetozone setosa* Malmgren, 1867 because it had spines in the neuropodia only: he was aware that *C. setosa* had rings of spines around the posterior segments because he had material, collected by MALMGREN, from Finmark (BMNH 1921.5.1.3226).

SOUTHERN (1914) described material from Clare Island, northwest Ireland, which he assigned to *Chaetozone zetlandica* after examining MCINTOSH's holotype. His collection included three forms, which he believed represented three different stages of development (Stages A, B and C; table and summary p.118). Six specimens of SOUTHERN's stage A, the smallest of the forms he described, were examined in the present study. The smallest individual is 5 mm by 0.5 mm for 43 chaetigers and the largest 6 mm by 0.5 mm for 75 chaetigers. The bidentate

Source : MNHN, Paris

FIG. 2. — *Caulleriella zetlandica* from Sullom Voe: **a**, anterior end, lateral view. **b**, cross section of posterior segment. **c**, slender capillary chaeta. **d**, stout awl-shaped capillary chaeta, medium length. **e**, stout awl-shaped capillary chaeta, short. **f**, spine with unidentate tip. **g**, spine with bidentate tip from indvidual of 5 mm length.

Source : MNHN, Paris

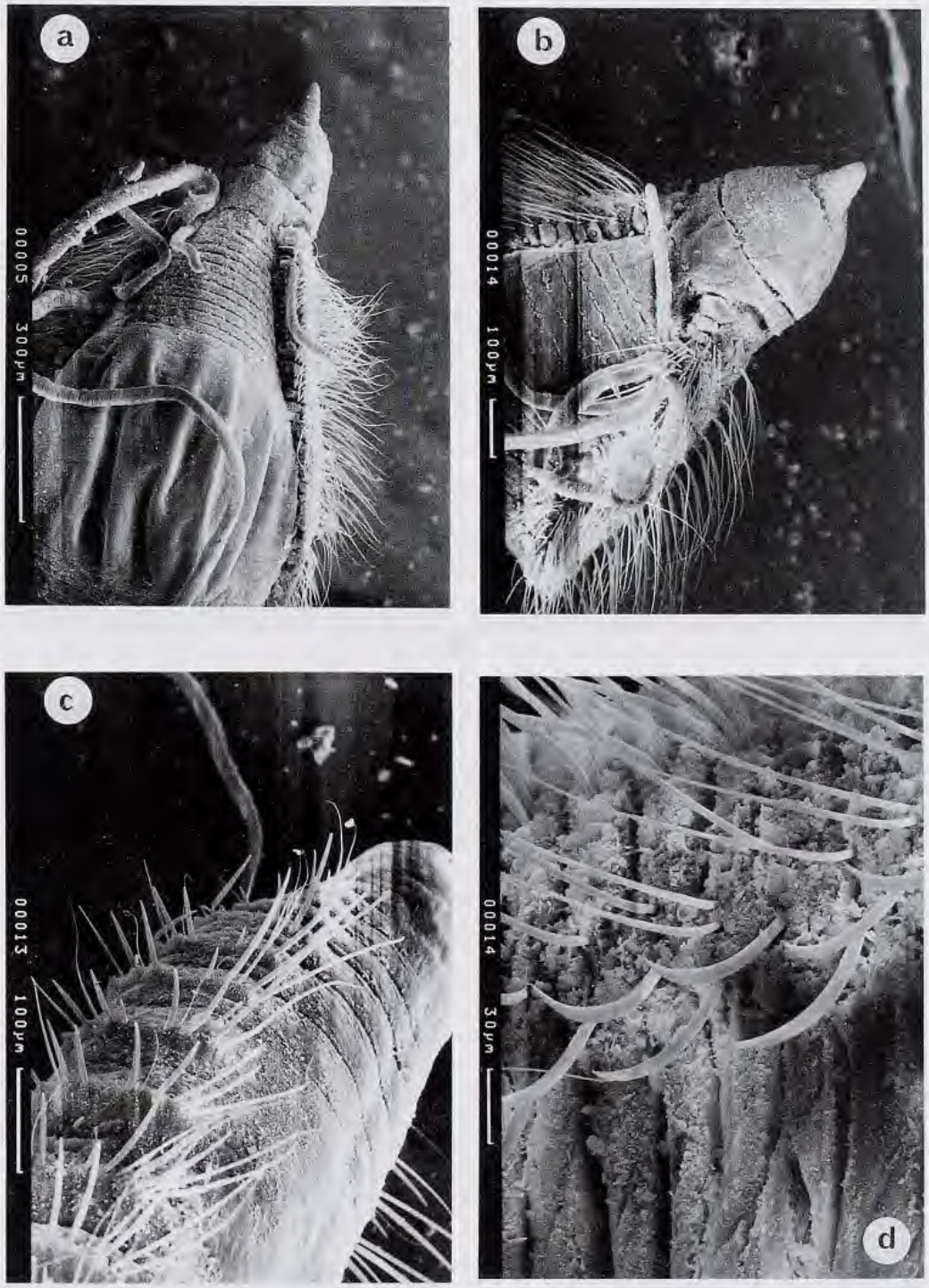



FIG. 3. — Scanning electron micrographs of *Chaetozone gibber* sp. nov.: **a**, anterior end, dorsal view showing position of hump. **b**, anterior end, dorsal view, showing arrangement of appendages (only stumps of tentacular palps present). **c**, posterior end, lateral view, showing arrangement of chaetae in notopodia and neuropodia. **d**, mid-body segments with stout awl-shaped capillary chaetae in notopodium.

Source : MNHN, Paris

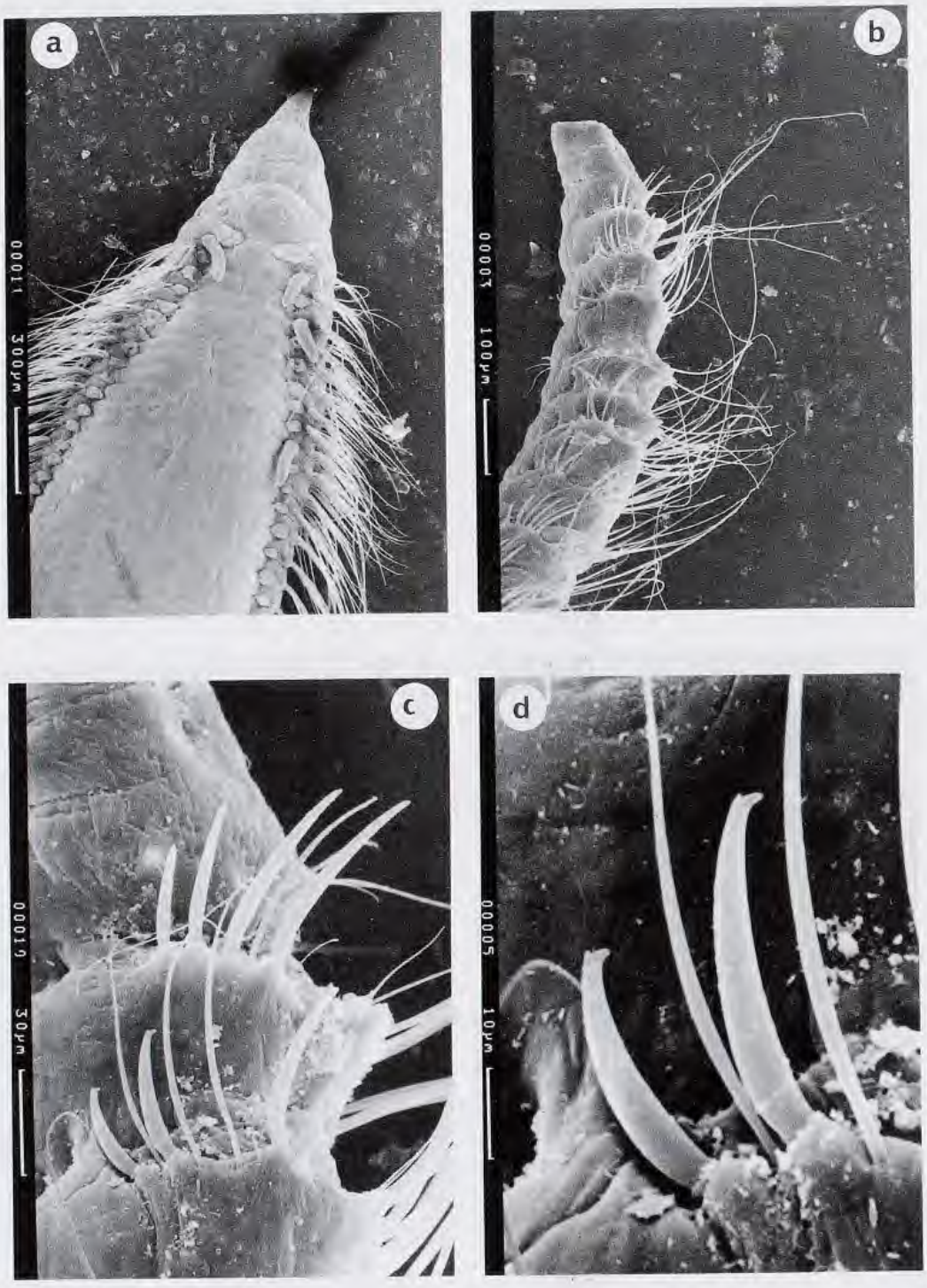



FIG. 4. — Scanning electron micrographs of *Caulleriella zetlandica* from Sullom Voe: **a**, anterior end, dorsal view, showing arrangement of appendages (only stumps of tentacular palps present) - **b** - **d**, posterior end, lateral view of small specimen (5 mm long) showing: **b**, presence of spines on neuropodium only - **c**, both unidentate and bidentate spines - **d**, bidentate spines from ventral side of neuropodium.

Source : MNHN, Paris

crochets (= spines) described and figured by SOUTHERN are clearly visible in the material examined and occur only in the neuropodium.

In his monograph McINTOSH (1915), expanding on his original description, figured one chaeta and mentioned the material of SOUTHERN (1914), but neither figured nor described bidentate chaetae. He suggested that his specimen obtained in July was a mature female, and that Southern's material was of a young pelagic form found between March and August.

Numerous specimens identified as *C. zetlandica* from Sullom Voe, very close to the type locality, were examined and compared with both McIntosh's fragment and Southern's material. The Sullom Voe material includes specimens ranging from 4 mm for 54 chaetigers to 24 mm for 154 chaetigers. The presence of bidentate spines on posterior segments of small specimens is confirmed (Figs 2g & 4d), together with the absence of such tips from larger specimens. Examination of a full size range of specimens has confirmed Southern's assumption that the three forms described by him represented different developmental stages of the same species. All of this material clearly belongs to the same species, which is distinguished from other members of the genus *Caulleriella* by the presence of acicular spines in the neuropodium only. Following HARTMAN (1961) and HARTMANN-SCHRÖDER (1971), the presence of bidentate hooks in small individuals, and lack of complete rings of spines, justify its continued placement within the genus *Caulleriella*, although the original diagnosis of this genus (CHAMBERLIN, 1919) included species with acicular chaetae in both neuropodia and notopodia.

## DISCUSSION

HARTMAN'S (1961) definitions of the bi-tentaculate cirratulid genera *Tharyx*, *Caulleriella* and *Chaetozone* are under review and have been partially revised by BLAKE (1991). As several authors have observed, all members of this group are similar in appearance, having a pointed prostomium, elongate peristomium bearing a pair of tentacular palps, and reduced parapodia. Currently these genera are separated according to the type and arrangement of the chaetae: these include smooth (*Aphelochaeta* Blake, 1991) or serrated (*Monticellina* Laubier, 1961) capillary chaetae only or, additionally, unidentate (*Chaetozone* Malmgren, 1867), knob-tipped (*Tharyx* Webster & Benedict, 1887) or bidentate (*Caulleriella* Chamberlin, 1919) spines. Spines, when present, can occur on the neuropodium only or on both rami, and may commence from the first chaetiger or (more commonly) further back; the arrangement of chaetae at the posterior end frequently being of key importance in identification.

The genus *Chaetozone* was erected for *C. setosa* Malmgren, 1867 but no generic diagnosis was included. Later workers (e.g. FAUVEL, 1927; BERKELEY & BERKELEY, 1952; HARTMANN-SCHRÖDER, 1971) have defined it as having a complete ring of unidentate spines on posteriormost segments; species with unidentate spines not arranged like this were referred to *Caulleriella* Chamberlin, 1919. DAY (1967) modified the definition slightly to those having spines in a continuous dorso-ventral arc. The definition of *Chaetozone* by HARTMAN (1961), however, includes all of the species with unidentate (entire) spines. CHRISTIE (1985) described populations of *"C. setosa"* in which the rings of spines are less than complete. The discovery of *C. gibber* and the apparent variability in form of *C. setosa*, together with the problems posed by species such as *C. zetlandica*, highlight the need for re-definitions of the genera *Chaetozone* and *Caulleriella*.

The status of *C. caputesocis* needs further examination. This species was transferred to *Caulleriella* by CHAMBERLIN (1919), but the definitions of HARTMAN (1961) suggest that, due to the presence of unidentate spines only, it should be referred to *Chaetozone*. Records of *C. caputesocis* from British waters need to be re-examined, and may be found to refer to *C. gibber*.

## ACKNOWLEDGEMENTS

The material from Folkestone and Sullom Voe was collected and processed by staff at ERT Ltd. We are grateful to the National Rivers Authority, Southern region, and to BP Petroleum Development Ltd., who commissioned the surveys at Folkestone and Sullom Voe respectively, for permission to use material and for supplying sediment data. We would like to thank Andrew S.Y. MACKIE (NMW) for loan of undescribed material. Additional material was kindly loaned by J.M.C. HOLMES (NMI), M. LOWE (BMNH), J.-C. DAUVIN (MNHN), J.-P. LECHAPT (MNHN, Dinard) and M. KENDALL (PML). We are very grateful to Andrew S. Y. MACKIE and Iain M. T. DIXON for discussions and suggestions on the manuscript, and to David HEPPELL for advice on

Source : MNHN, Paris

nomenclature, Paul WILTHEW for assistance with SEM, Graham CLARK for printing the photographs, Dorothy HARTLEY for assistance with word processing and Sue HAMILTON for proof-reading.

## REFERENCES

BERKELEY, E. & BERKELEY, C., 1952. — *Canadian Pacific Fauna. 9, Annelida. 9b (2), Polychaeta Sedentaria.* Fisheries Research Board of Canada, The University of Toronto Press, Toronto, 139 pp.

BLAKE, J. A., 1991. — Revision of some Genera and Species of Cirratulidae (Polychaeta) from the Western North Atlantic. *Ophelia Suppl.*, **5** : 17-30.

CHRISTIE, G., 1985. — A comparative study of the reproductive cycles of three Northumberland populations of *Chaetozone setosa* (Polychaeta: Cirratulidae). *J. mar. biol. Ass. UK.*, **65** : 239-254.

CHAMBERLIN, R. V., 1919. — The Annelida Polychaeta. *Mem. Mus. comp. Zool. Harv.*, **48** : 1-514.

DAY, J., 1967. — A monograph on the Polychaeta of Southern Africa. Part 2 Sedentaria. *Trustees of the British Museum (Nat. Hist.)*, London : 459-878.

FAUVEL, P., 1927. — Polychètes Sédentaires. *Faune Fr.* **5** : 1-494.

HARTMAN, O., 1961. — Polychaetous Annelids from California. *Allan Hancock Pacif. Exped.*, **25** : 1-226.

HARTMANN-SCHRÖDER, G., 1971. — Annelida, Borstenwürmer, Polychaeta. *Tierwelt Deutschlands und der angrenzenden Meeresteile* **58** : 1-594.

HOWSON, C. M., HARTLEY, J. P., MACKIE, A. S. Y. & O'CONNOR, B., 1987. — Annelida. *In:* C.M. HOWSON (ed), *Directory of the British Marine Fauna and Flora.* Marine Conservation Society, Herefordshire, pp. 76-123.

IBANEZ, I. & DAUVIN, J.-C., 1988. — Long-term changes (1977 to 1987) in a muddy fine sand *Abra alba-Melinna palmata* community from the western English Channel: multivariate time-series analysis. *Mar. Ecol. Prog. Ser.*, **49** : 65-81.

LAUBIER, L., 1961. — *Monticellina heterochaeta* n. g., n. sp., Cténodrilide (Polychètes Sédentaires) des vases côtières de Banyuls-sur-Mer. *Vie Milieu*, **11** : 601-604.

LECHAPT, J-P., 1983. — *Chaetozone setosa* Malmgren, 1867 (Annelida Polychaeta Cirratulidae). Observations en Rance Maritime. Étude morphologique. Position systématique. *Bulletin Soc. Sci. Bretagne*, **55** : 25-30.

MALMGREN, A. J., 1867. — Annulata Polychaeta Spetsbergiae, Groenlandiae, Istandiae et Scandinaviae hactenus cognita. *K. Vetenskakad. Förh. Stockh.*, **24** : 127-235.

McINTOSH, W. C., 1911. — Notes from the Gatty Marine Laboratory, St. Andrews. No XXXII. *Ann. Mag. nat. Hist.*, **7** : 145-173.

McINTOSH, W. C., 1915. — *A monograph of the British marine Annelids. 3 Polychaeta, Ophelidae to Ammocharidae.* Ray Society, London, 368 pp.

SAINT-JOSEPH (Baron de), A., 1894. — Les Annélides polychètes des Côtes de Dinard. 1st Part. *Annls. Sci. nat., 7th series, 3rd part.*, **17** : 1-395.

SOUTHERN, R., 1914. — Clare Island Survey. Part 47. Archiannelida and Polychaeta. *Proc. Roy. Ir. Acad.*, **31** : 1-160.

WEBSTER, H. E. & BENEDICT, J.E., 1887. — The Annelida Chaetopoda from Eastport, Maine. *Rep. U.S.Commis. Fish.* 1885 : 707-755.

Source : MNHN, Paris

# Phylogeny of Alciopidae (pelagic polychaetes): a cladistic analysis

*Baoling WU & Lua HUA*

Department of Marine Biology, First Institute of Oceanography of SOA
Hongdao Road 13, Qingdao 266003, P. R. China

ABSTRACT

The phylogenetic relationships of the nine genera in the family Alciopidae are reexamined using a cladistic analysis. Three phyllodocid genera *Eulalia*, *Phyllodoce* and *Notophyllum* are used as outgroups to polarize the 13 morphological characters. The results indicate that the nine genera can be divided into two groups which agrees with the ideas of STOP-BOWITZ (1948) and RICE (1987). It is proposed that two subfamilies can be recognized in the Alciopidae: (1) Watelinae, which includes the genera *Alciopina*, *Krohnia*, *Plotohelmis*, *Rhynchonerella* and *Watelio*, and (2) the Alciopinae, containing the genera *Alciopa*, *Naiades*, *Torrea* and *Vanadis*.

RÉSUMÉ

**Phylogénie des Alciopidae (polychètes pélagiques): une analyse cladistique**

Les relations phylogénétiques de neuf genres de la famille des Alciopidae sont réexaminées à l'aide de l'analyse cladistique. Trois genres de phyllodociens *Eulalia*, *Phyllodoce* et *Notophyllum* sont utilisés comme groupes extérieurs pour polariser les 13 caractères morphologiques. Il apparaît que les neuf genres peuvent être divisés en deux groupes, ce qui est en accord avec les idées de STOP-BOWITZ (1948) et RICE (1987). On propose que les Alciopidae soient partagées en 2 sous-familles: (1) Watelinae, incluant les genres *Alciopina*, *Krohnia*, *Plotohelmis*, *Rhynchonerella* et *Watelio*, et (2) Alciopinae, incluant les genres *Alciopa*, *Naiades*, *Torrea* et *Vanadis*.

## INTRODUCTION

The pelagic family Alciopidae is composed of nine genera which spend their entire life in the water column (RICE, 1987). Genera in this family include *Alciopa*, *Alciopina*, *Krohnia*, *Naiades*, *Plotohelmis*, *Rhynchonerella*, *Torrea*, *Vanadis* and *Watelio*. Alciopid polychaetes form a monophyletic group as indicated by the two large telescopic eyes. This characteristic is not found in other polychaetes. Alciopids also possess five small cephalic tentacles, an eversible proboscis with soft marginal papillae or two lateral horns, 3-5 pairs of tentacular cirri in the three anterior segments, uniramous parapodia and a transparent to semitransparent body.

WU, B.L., & L. HUA, 1994. — Phylogeny of Alciopidae (pelagic polychaetes): a cladistic analysis. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 317-321. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

Two major views on the evolutionary relationships among the nine genera of Alciopidae have been proposed. The first view, represented by HERING (1892), APSTEIN (1900) and STOP-BOWITZ (1948), is that the Alciopidae can be divided into two groups: (1) in the first group the proboscis has two long lateral horns, females with one or two pairs of receptacula seminis, setae of only one type, either simple or compound. This group includes *Alciopa*, *Naiades*, *Torrea* and *Vanadis*. (2) The second group the proboscis lacks lateral horns, females lack receptacula seminis, and at least two kinds of setae are present. This group includes *Alciopina*, *Plotohelmis*, *Krohnia*, *Rhynchonerella* and *Watelio*.

DALES (1955) also places the nine genera into two groups based on setal type. The first group only has simple setae and contains *Alciopina* and *Krohnia*. The second group possesses compound setae except, for Naiades, which has only simple setae, and includes *Alciopa*, *Naiades*, *Plotohelmis*, *Rhynchonerella*, *Torrea* and *Vanadis*. The genus *Watelio* is intermediate between the two groups.

Recently, RICE (1987) has utilized morphological and reproductive characters in his study of generic relationship in the Alciopidae. His results fully with those of STOP-BOWITZ (1948). The purpose of this study is to use cladistic methods to reevaluate the phylogenetic relationships of alciopid genera.

## MATERIAL AND METHODS

Thirteen morphological characters were used in the present analysis, all of which have been used in traditional alciopid taxonomy (STOP-BOWITZ, 1948; FAUVEL, 1953; DALES, 1957; TEBBLE, 1960; DAY, 1967; USCHAKOV, 1972; WU, 1978; RICE, 1987). The character states of the alciopid genera and of the outgroups are listed in Tables 1 and 2. All character states are consistent among a genus except for the proboscis of *Vanadis longissima* which has small marginal papillae but no lateral horns. The other 12 species of *Vanadis* have lateral horns, and we treat the proboscis of all *Vanadis* as having lateral horns.

Prostomium and Eyes (I-II): Alciopidae are characterized by two large eyes with red lenses which may be directed anteriorly, laterally, upward or downward. This character is chosen to distinguish the nine alciopid taxa from the outgroup. The prostomium of some genera extends in front of the eyes, but in others the eyes project forward, with the small prostomium between them.

Proboscis (III-V): The eversible proboscis of Alciopidae is either long or relatively short, some with soft marginal papillae or two lateral horns which are provided with mucus secreting cells (DALES, 1955).

Tentacular cirri (VI): There are 3-5 pairs of tentacular cirri in the first three segments, the formula is (USCHAKOV, 1972): 1+1/0 or 1+1/0 or 1 or N, in which 1 = tentacular cirrus, 0 = tentacular cirrus absent, N = normal podial cirrus.

Parapodia and receptacula seminis (VII-VIII): Several anterior parapodia are reduced in some alciopid genera but fully developed in the others. All normal parapodia are uniramous. Mature females of some genera, such as *Vanadis*, often bear 1-2 pairs of dorsal cirri (from segment 4-5) modified into receptacula seminis for reproduction.

Setae (IX-XI): Four types of setae occur in alciopids, they are capillaries, simple aciculae, compound aciculae and compound spinigers. Some genera have either capillaries or spinigers; others may possess two or three kinds of setae.

Distal paraodial cirrus (XII): one or two cirriform terminal appendages often exist at the distal end of the podial lobe of some alciopid genera.

Body transparency (XIII): Some genera such as *Alciopa*, *Alciopina* and *Rhynchonerella* have strong muscular bodies and are semitransparent to opaque when alive. The other six genera lack such a developed muscular system and have transparent bodies.

The alciopids clearly arose from benthic phyllodocids somewhat like the present day phyllodocid genus *Eulalia* (DALES, 1955; USCHAKOV, 1972). PLEIJEL (1991) used cladistic analysis to divide the family Phyllodocidae into three subfamilies in which the genera *Eulalia*, *Phyllodoce* and *Notophyllum* occupied the central position. These three genera were selected as outgroups to polarize the 13 characters.

The BRANCH AND BOUND algorithm from the phylogenetic computer package PAUP (version 2.4.1, David L. Swofford, Ill. State Nat. Hist. Surv., Urbana 61820) was used to find out the most parsimonious trees. All of the multistate characters are treated as ordered. All characters were given equal weight. The IBM computer at the First Institute of Oceanography was also used in this work.

Source : MNHN, Paris

## RESULTS AND DISCUSSION

Thirty-three cladograms obtained, all with a consistency index of 0.60 and a length of 25 steps. But there is only one cladogram (Fig. 1) with the lowest F value of 0.201, So only this cladogram has been chosen to do the analysis work. The analysis indicates:

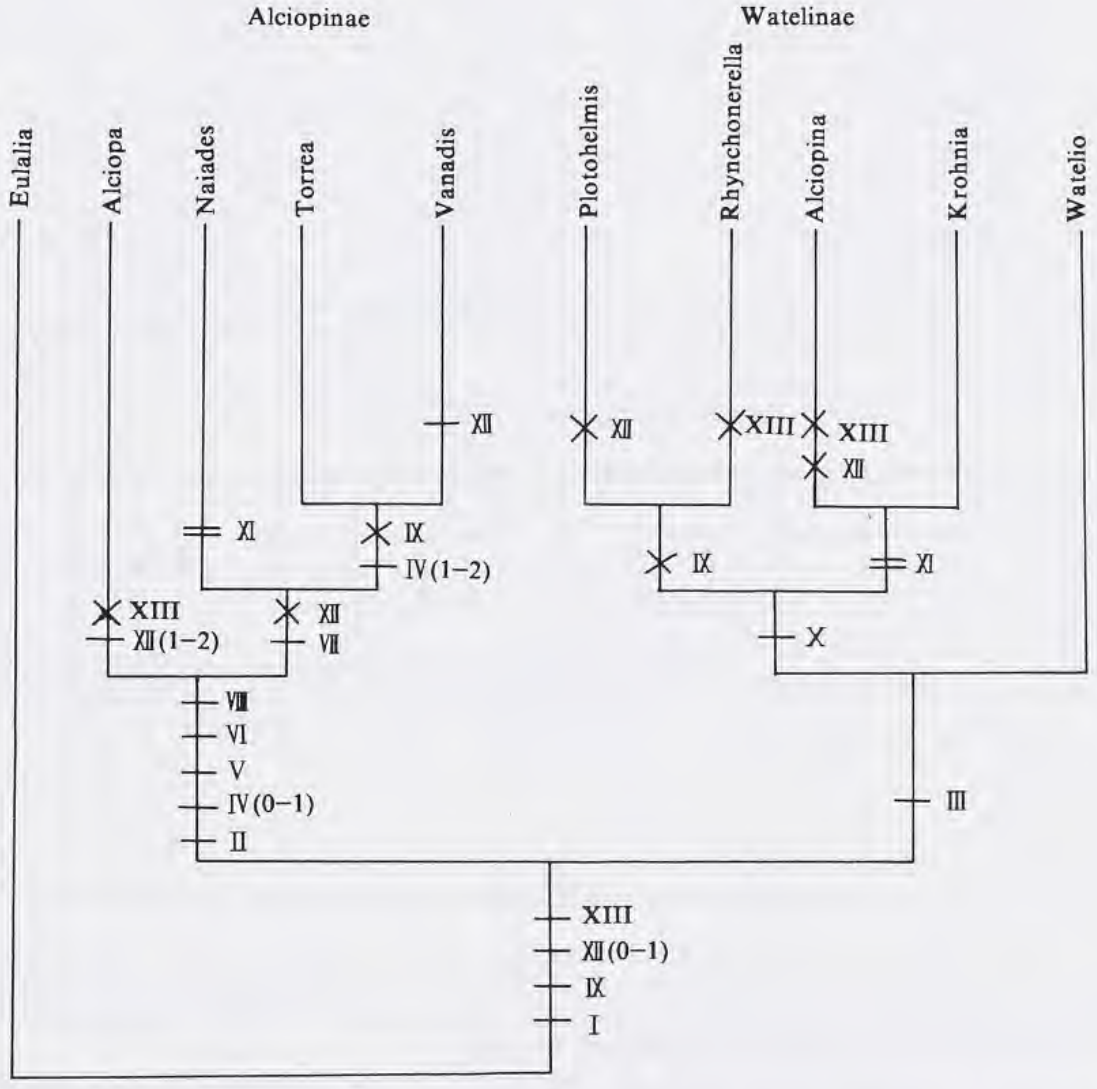



FIG. 1. — Cladogram of the Alciopidae, with phyllodocid genus *Eulalia* as outgroup. Consistency index is 0.600, F value is 0.201. Progression = "—", regression = "X", Parallelism = "=" . Numbers in parentheses indicate character-state changes in multistate characters, e.g., IV (1-2) indicates that character IV goes from state 2 to state 3.

1. The plesiomorphic character states for the common hypothetical ancestor of the nine alciopid genera are: The prostomium project in front of the eyes; the eyes are enlarged; the sucking proboscis with soft papillae but no lateral horns; the second ventral cirri present; the parapodia uniramous and all fully developed; both capillaries and compound spinigers setae present; one distal parapodia cirrus present; with transparent body. It is very clear that this hypothetical alciopid ancestor lived a pelagic life, but it still leaves some primitive features similar to its ancestral benthic form.

Source : MNHN, Paris

TABLE 1. — Coding of morphological characters for the alciopid genera. The numbers correspond to those in the data matrix in Table 2 and the cladogram in Fig. 1.

| | | | | |
|---|---|---|---|---|
| I. | Enlarged eyes: | 0:Absent | 1-Present | |
| II. | Prostomium projecting in front of the eyes: | 0-Yes | 1-No | |
| III. | Proboscis length: | 0-Long | 1-Short | |
| IV. | Lateral horns on proboscis: | 0-Absent | 1-Short; | 2-long |
| V. | Papillae on proboscis: | 0-Present | 1-Absent | |
| VI. | Second pair of ventral tentacular cirri: | 0-Present | 1-Absent | |
| VII. | Reduced parapodia: | 0-Absent | 1-Present | |
| VIII. | Receptacula seminis: | 0-Absent | 1-Present | |
| IX. | Capillaries setae: | 0-Absent | 1-Present | |
| X. | Simple acicula setae: | 0-Absent | 1-Present | |
| XI. | Compound spinigers setae: | 0-Present | 1-Absent | |
| XII. | Distal parapodial cirrus: | 0-Absent | 1-One present | 2-Two present |
| XIII. | Body transparency: | 0-Opaque | 1-Transparent | |
| | | to semitransparent | | |

TABLE 2. — Matrix of character states of the nine alciopid genera and their outgroup. The numbers correspond to those in Table 1 and Fig. 1.

| Characters OIU | I | II | III | IV | V | VI | VII | VIII | IX | X | XI | XII | XIII |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eulalia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Vanadis* | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Naiades* | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Torrea* | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Plotohelmis* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Rhynchonerella* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Alciopa* | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 |
| *Alciopina* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Watelio* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| *Krohnia* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |

2. The family Alciopidae can be divided into two major groups and the division pattern agrees with STOPBOWITZ (1948) and RICE (1987) rather than by DALES (1955). The two subgroups are all monophyletic ones specified by several characteristics. In order to express the phylogenetic relationships among alciopid genera clearly, we suggest that two subfamilies exist within Alciopidae.

(1) Alciopinae. Contains four genera: *Alciopa*, *Naiades*, *Torrea* and *Vanadis*. Their common hypothetical ancestor is as follows: prostomium does not extend anterior to the eyes; the eversible proboscis with lateral horns but lacks soft papillae; second pair of ventral tentacular cirri absent; females with one or two pairs of receptacula seminis, parapodia with capillaries and compound spinigers setae, and one podial cirrus.

(2) Watelinae. Contains five genera: *Alciopina*, *Krohnia*, *Plotohelmis*, *Rhynchonerella* and *Watelio*. Their common hypothetical ancestor is similar to the genus *Watelio* and has the following characteristics: proboscis relatively short; no lateral horns; females lacking special receptacula seminis; parapodia with capillaries and compound spinigers setae and one podial cirrus; body transparent.

3. Alciopidae can not be divided into subgroups based on setae type. However, in the evolution of the family into subfamilies, this character changes greatly which gives it an important status in genus classification. Finally it should be emphasized that the above views need testing when more information on alciopids are available, which will make it possible to do a cladistic analysis at the species level.

Source : MNHN, Paris

## ACKNOWLEDGEMENTS

We wish to thank Prof. Ju-Shey HO of California State University, Long Beach, USA for providing us the PAUP program. Special thanks are due to Mrs. Wang XUEMEI and Mr. Mu HONG-LIN for typing this paper. This research is supported by a grant from National Natural Science Foundation of China, number 3870080.

## REFERENCES

APSTEIN, C., 1900. — Die Alciopiden und Tomopteriden der Plankton Expedition. *Ergeb. Plankt. Exped.*, **11** : 1-61.

DALES, R.P., 1955. — The evolution of the pelagic alciopid and phyllodocid polychaetes. *Proceed. Zool. Soc. London*, **125** : 411-420.

DALES, R.P., 1957. — Pelagic polychaetes of the Pacific Ocean. *Bull. Scripps Instit. Oceanogr.*, **7** : 95-167.

DALES, R.P. & G. PETER, 1972. — A synopsis of the pelagic polychaeta. *J. nat. Hist.*, **6** : 55-92.

DAY, J.H., 1967. — *Polychaete of Southern Africa*. Part 1. Errantia. British Museum (Natural History) London, 458pp.

FAUVEL, P., 1953. — *The Fauna of India. Annelida Polychaeta*. Allahabad, 507pp.

HERING, E., 1892. — Zur Kenntnis der Alciopiden von Messina. *Sitzb. K. Akad. Wiss. Wien. Math. nat. Kl*, **101** : 713-768.

PLEIJEL, F., 1991. — Phylogeny and classification of the Phyllodocidae (Polychaeta). *Zool. Scr.*, **20** : 225-261.

RICE, S. A., 1987.— Reproductive Biology, Systematics, and evolution in the polychaete family Alciopidae. *Biol. Soc. Wash. Bull.*, **7** : 114-127.

STOP-BOWITZ, C., 1948. — Polychaete from the Michael Sars North- Atlantic Deep-Sea Expedition 1910. *Rep. scient. Res. "Michael Sars" North-Atlantic Deep-Sea Exped.*, **5** : 1-91.

TEBBLE, N., 1960. — The distribution of pelagic polychaetes in the South Atlantic Ocean. *Discovery Rep.*, **30** : 161-300.

WILEY, E.O., 1981. — *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, Inc., New York, 439 pp.

USCHAKOV, P.V., 1972. — *Polychaetes, Vol. 1. Fauna of USSR*. Akademia Nauk, Zoological Institute, Series N°**102**, 259 pp.

WU, B.L. & SUN, R., 1978. — Preliminary studies on geographical distribution and evolution of pelagic polychaetes from South China Sea Islands. *Oceanol. Limnol. Sinica*, **9** : 215-223.

Source : MNHN, Paris

Source : MNHN, Paris

# Preliminary observations on a dense population of *Phyllochaetopterus socialis* Claparède at the sulphurous water boundary in a Mediterranean submarine cave

*Marco ABBIATI*, L. AIROLDI*, Alberto CASTELLI**, F. CINELLI * & A.J. SOUTHWARD ****

* Dipartimento di Scienze dell'Ambiente e del Territorio, Università di Pisa, Via Volta 6, I-56126 Pisa, Italy
** Istituto di Scienze Antropologiche, Università di Sassari, Via Margherita di Savoia 15, I-07100 Sassari, Italy
*** Leverhulme Unit, Marine Biological Association of the U. K., Citadel Hill, Plymouth, PL1 2PB, U.K.

ABSTRACT

The Grotta Sulfurea (Sulphurous Cave) at Capo Palinuro, southern Tyrrhenian Sea, is characterised by the presence of springs of sulphide-rich water. The issuing water accumulates below the roof of the cave and supports thick mats of *Beggiatoa* -type sulphur bacteria. A dense assemblage of *Phyllochaetopterus socialis* was found in the inner part of the cave, where the sulphurous water extends to the bottom. Specimens showed peculiar morphological features. They occurred immediately below the sulphurous boundary and their tubes extended into the sulphurous water. There was a thick layer of filamentous sulphur bacteria on the tubes. The abundance of the *P. socialis* assemblage in the Grotta Sulfurea appeared to be related to the presence of the sulphide springs and the growth of sulphur bacteria. Preliminary results of stable carbon isotope analyses on *P. socialis* support the hypothesis that most of the worm's carbon comes from bacteria.

RÉSUMÉ

**Observations préliminaires sur des populations denses de *Phyllochaetopterus socialis* Claparède à la limite des eaux sulfureuses dans une grotte sous-marine méditerranéenne**

La grotte "Grotta Sulfurea" (Cap Palinuro, Mer Tyrrhénienne méridionale) est caractérisée par une circulation d'eau riche en sulfures qui s'accumule au-dessous de la voute de la grotte et permet le développement d'une épaisse couche de bactéries chimiosynthétiques. Dans la partie la plus interne, où le fond de la grotte remonte au niveau de l'eau sulfureuse, un peuplement dense à *Phyllochaetopterus socialis* a été découvert. Les individus vivent immédiatement en dessous des eaux sulfureuses; leurs tubes sont recouverts de bactéries. On pense que la forte densité du peuplement à *P. socialis* est en relation avec la présence de la source sulfureuse. Les résultats préliminaires de l'analyse des sources de carbone sur *P. socialis* confirment cette hypothèse.

---

ABBIATI, M., AIROLDI, L., CASTELLI, A., CINELLI, F. & A.J. SOUTHWARD, 1994. — Preliminary observations on a dense population of *Phyllochaetopterus socialis* Claparède at the sulphurous water boundary in a Mediterranean submarine cave. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 323-329. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

The biological communities inhabiting hydrothermal vents at mid-ocean ridges have been studied intensively in recent years (DESBRUYÈRES *et al.*, 1985; GRASSLE, 1985; JANNASCH, 1985; SOUTHWARD, 1989; TUNNICLIFFE, 1991; CHILDRESS & FISHER, 1992). Hydrothermal environments that occur in shallow-water provide an opportunity to study such complex systems at sites with easier access than mid-ocean ridges (TARASOV *et al.*, 1990). We carried out preliminary surveys of a marine cave system at Capo Palinuro (southern Tyrrhenian Sea) in connection with an international co-operative study devoted to shallow-water hydrothermal communities. This system includes several caves characterised by the presence of underwater sulphurous springs (ABBIATI *et al.*, 1992) which support dense mats of *Beggiatoa*-like sulphur bacteria. During our surveys a dense assemblage of the tube-dwelling chaetopterid polychaete *Phyllochaetopterus socialis* Claparède was found in the Grotta Sulfurea where it occurred at the boundary between sulphurous water and sea-water.

Submarine caves are usually considered to be oligotrophic environments with reduced fauna and flora and low biomass (OTT & SVOBODA, 1976; HARMELIN *et al.*, 1985; FICHEZ, 1990). The abundance of *P. socialis* in the Grotta Sulfurea appeared unusual. It was hypothesized that this abundance was related to bacterial chemosynthetic production which was supplementing the meagre input from photosynthetic sources. Investigations are in progress to verify this hypothesis and to study the complex trophisms of the Grotta Sulfurea and similar sulphurous caves.

The abiotic and biological features of the cave and the morphological variability and possible food sources of *P. socialis* are presented in this paper.

## ECOLOGY AND DISTRIBUTION OF *PHYLLOCHAETOPTERUS SOCIALIS*

*Phyllochaetopterus socialis* Claparède 1868 is a gregarious species belonging to the family Chaetopteridae. In the original description from the Gulf of Naples CLAPARÈDE (1868) pointed out that it occurred in high densities and considered it to be the most abundant polychaete in the Gulf of Naples. *P. socialis* occurs from 10 m to more than 300 m in depth on different substrates (muddy bottoms, organogenic sand and hard bottoms) where it often forms dense mats. It has been reported from several different geographical regions: Mediterranean Sea (FAUVEL, 1927; BELLAN, 1964; LAUBIER, 1966; REYSS, 1971; BHAUD, 1974, 1977; BHAUD & AMOUROUX, 1975), Atlantic Ocean (DAY, 1967, 1973; Mc CARTY, 1974; GETTLESON *et al.*, 1985), Pacific Ocean (GIBBS, 1971), Indian Ocean (DAY, 1967). This wide geographic and bathymetric distribution indicates a cosmopolitan species (GETTLESON *et al.*, 1985) although there are questions concerning the validity of some records (BHAUD, 1977).

## MATERIAL AND METHODS

STUDY SITE. — The Grotta Sulfurea is located at Capo Palinuro (southern Tyrrhenian Sea) (Fig. 1). It is a narrow sloping tunnel that opens into carboniferous rocks. It is characterised by the presence of springs of sulphide-rich water, normally warmer than ambient sea-water and of lesser salinity. This less dense water accumulates below the roof of the cave giving rise to a thermal oxic-anoxic interface. Preliminary data on the speleological characteristics of the cave are reported by MUSCIO (1985) and MUSCIO & SELLO (1989).

SAMPLING METHODS. — The Grotta Sulfurea cave was sampled in May 1991 and May 1992 by SCUBA diving. A detailed survey of the cave as far as 40 m inside the entrance was carried out following the procedures of ALVISI (1991). A permanent 40 m long transect was established by means of a tape line. Changes in the composition and richness of the biological community along the transect were investigated by visual and photographic surveys. Outside-inside light gradient was measured by means of an irradiance meter (Biospherical Instruments Inc., QSI 140). Temperature and salinity vertical gradients across the sulphurous water boundary were surveyed at point D (Fig. 1). Temperature was measured from 5.5 to 9.5 m in depth by means of an underwater digital thermometer (Idronaut Srl). Water samples for salinity measurement were collected across the sulphurous water boundary by means of eight 20 ml syringes spaced every 15 cm on a one meter long Plexiglas bar. Salinity of the samples was estimated from readings of a portable sodium electrode (Horiba Compact Salt Meter, C-121). Dissolved sulphide in water samples from the sulphurous layer was estimated by the method of CLINE (1969). Specimens of *P. socialis* were collected and fixed in buffered 4 % formalin for later analysis. Other

Source : MNHN, Paris

specimens and samples of the bacterial mats were treated with 10 % HCl, dried at 50 °C and powdered for stable carbon isotope analysis.

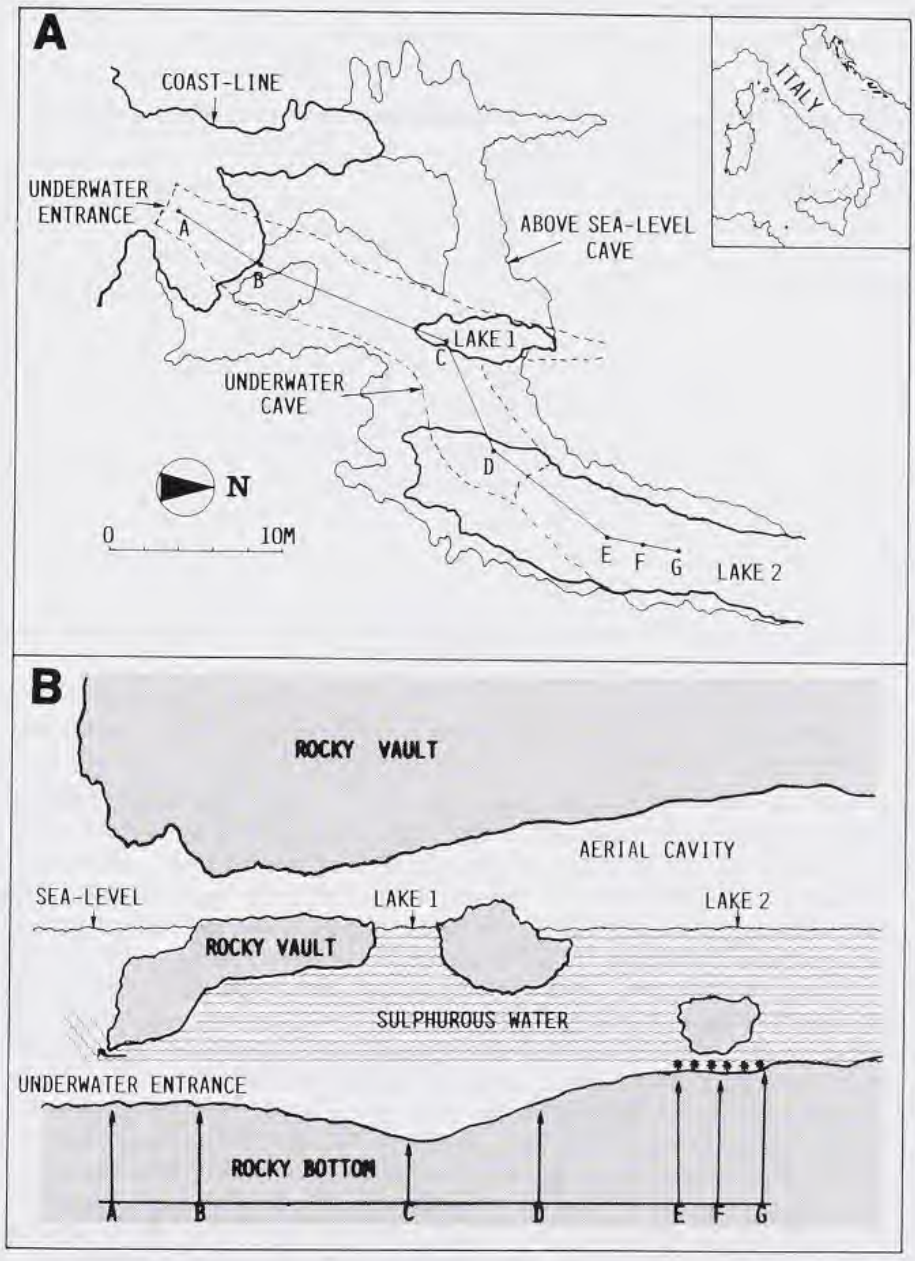



FIG. 1. — Location of Grotta Sulfurea cave (Tyrrhenian Sea, Italy). A, plan of the cave and location of the transect. B, longitudinal section of the cave (plotted along points A, B, C, D, E, F, G).*P. socialis* assemblage (asterisks) occurs at points E, F and G.

## RESULTS

The peculiarity of the Grotta Sulfurea is the occurrence of sulphide-rich waters. The source of the sulphurous spring outlets was not determined since they arise in the innermost part of the cave which is difficult and dangerous to explore. The sulphurous water, which was lower in density than normal sea-water, accumulated

Source : MNHN, Paris

below the vault of the cave (Fig. 1,B). The temperature and salinity measurements across the sulphurous-water/sea-water interface indicated a sharp thermo- chemocline. Temperature and salinity values ranged from 18.7 °C and 36.5 P.S.U. to 25.9 °C and 30 P.S.U. in the sea-water and in the sulphurous water, respectively (Fig. 2). Preliminary analyses of the sulphurous water in May 1992 indicated millimolar levels of dissolved sulphide compared with zero below the interface.

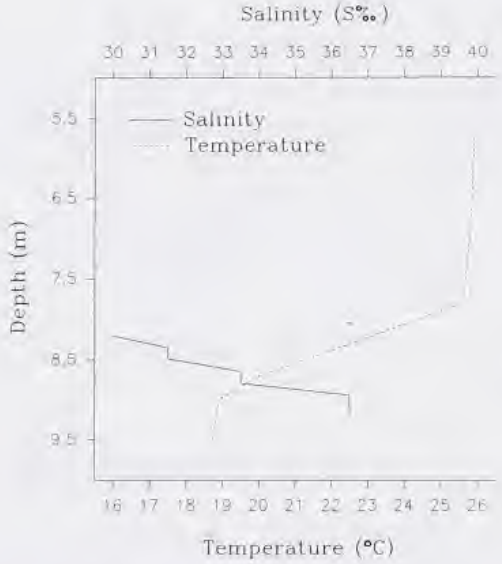



FIG. 2. — Temperature (°C) and salinity (P.S.U.) vertical gradients at the sulphurous boundary level.

The sulphurous water boundary was located at about 8.7 m and separated two different biological assemblages. White bacterial mats lined the rocky surface which was in contact with the sulphurous water. The thick *Beggiatoa*-like mats thinned out near the boundary between the sulphurous water and normal sea-water. Large numbers of a small tubificid oligochaete were found within the thick bacterial mats. Below the thermo-chemocline a reduced benthic community occurred which showed a decrease of the number of species and specimens towards the inside of the cave. At the entrance of the cave (Fig. 1, point A) light was 3.88 E 14 quanta. $cm^{-2}$. $sec^{-1}$ and crustose coralline algae were present. At point B and C (Fig. 1) the light was reduced to 5 % and to 1%, respectively. Total darkness occurred at point D, and a reduced community was observed on the walls of the cave (sponges and scleractinians) and bottom (ophiuroids). In the completely dark inner part of the tunnel (Fig. 1, points E, F, G) at about 8.7 m in depth the sulphurous water extended to the bottom. Just to the seaward of this level, where the tunnel deepened and the chemocline began to lift off the bottom, there were thick aggregates of *P. socialis* on the bottom and sides of the cave (Fig. 1). The worm colonies were composed of several hundred individuals and covered all the boundary belt where the sulphurous water mixed with the sea-water. The tubes were about 10 cm long, and the worm's tentacles extended just into the sulphurous water. The tubes were covered with a layer of filamentous bacteria which became thicker near the distal end of the tubes. Beyond point G (Fig. 1) the walls and the bottom were completely covered by bacterial mats inhabited by oligochaetes. One specimen of the anthozoan *Alicia mirabilis* was found on the bottom.

Morphological analysis of the specimens agreed with the original description of *P. socialis* (CLAPARÈDE, 1868) and with the redescription by BHAUD & AMOUROUX (1975) and BHAUD (1977). *P. socialis* is characterised by one stout specialised seta on setiger IV. The morphology of the modified seta agreed with the description by BHAUD (1977: 210, Fig. 1c-d). However, variability in the number of the stout setae was observed in the Grotta Sulfurea specimens; a few individuals (about 5 %) had two stout setae at the setiger IV or one stout setae in both the setigers IV and V. When two setae were present in the same segment, the second seta appeared slightly thinner and longer than the typical one. The number of setigers in the anterior region of *P. socialis* ranges from 10 to 18 with 13-14 usually present (FAUVEL, 1927; DAY, 1967; BHAUD & AMOUROUX, 1975). In the population the

Source : MNHN, Paris

number of setigers ranged from 13 to 18 with 15 the most common. About 60% of the individuals had a different number of setigers on the left and right side of the body (Table 1). The number of setigers in the posterior region of the body ranged from 10 to 20 which agreed with previous descriptions (CLAPARÈDE, 1868; FAUVEL, 1927; DAY, 1967; BHAUD & AMOUROUX, 1975).

TABLE 1. — Setiger number in the anterior region of the body in Grotta Sulfurea specimens of *P. socialis* (N = 129)

| | N° parapodia | | N° specimens | % |
|---|---|---|---|---|
| Symmetric | 14 | 14 | 14 | 10.8 |
| specimens | 15 | 15 | 40 | 31.0 |
| | 16 | 16 | 5 | 3.9 |
| Total | | | 59 | 45.7 |
| Asymmetric | 13 | 14 | 5 | 3.9 |
| specimens | 13 | 15 | 2 | 1.6 |
| | 14 | 15 | 30 | 23.2 |
| | 14 | 16 | 2 | 1.6 |
| | 15 | 16 | 22 | 17.0 |
| | 15 | 17 | 1 | 0.8 |
| | 16 | 17 | 7 | 5.5 |
| | 16 | 18 | 1 | 0.8 |
| Total | | | 70 | 54.3 |

Carbon isotope analyses were carried out in Texas by Dr M.C. KENNICUTT. There was much depletion of the heavy isotope in the tissues of *P. socialis*, and a similar depletion was shown by the bacterial mats. The similarity of the values ($^{13}C$ depletions of -30.1 and -30.9, as parts per thousand compared with the usual PDB standard) indicates close trophic coupling.

## DISCUSSION

The high density of *P. socialis* in the inner part of the Grotta Sulfurea is unusual for a submarine cave. As already noted, typical submarine caves show a reduction in the biota along a gradient from outside to inside (OTT & SVOBODA, 1976; HARMELIN *et al.*, 1985; FICHEZ, 1990, 1991). This decrease corresponds to the decrease in photosynthetic production and of penetration of food particles from the sea. This biological gradient was noted on substrata in contact with the sea-water. In contrast, surfaces washed by the sulphurous water were covered by thick mats of sulphur bacteria. The bacteria were mostly different kinds of the genus *Beggiatoa* and contained much elemental sulphur which is typical for the group. The preliminary assumption is that there is high chemoautotrophic production by the bacteria which use energy obtained by oxidation of sulphide.

We can presume that the high biomass of *P. socialis* is related to the bacterial production which provides a food source. The abundant biota at other deep sea and shallow-water hydrothermal habitats are also supported by chemoautotrophic production either by free-living bacteria or by symbiotic bacteria, based on the mixing of vent water containing reduced sulphur with oxygenated sea-water (SOUTHWARD, 1987; FISHER, 1990; CHILDRESS & FISHER, 1992). In the Grotta Sulfurea the localised position of the colonies of *P. socialis* in the transition zone between the sulphurous water and sea-water points to the need for a combination of the same extremes - reduced sulphur and oxygen - for sustenance. The stable carbon isotope values indicate that the bacteria provide the main or only food source for *P. socialis*; however, it is not yet clear exactly how the worms feed on the bacteria.

The Grotta Sulfurea population of *P. socialis* showed considerable morphological variation. The specialized stout setae on the setiger IV is one of the primary taxonomic characters in *P. socialis*. It is considered to be unaffected by morphological variations in relation to different geographic localities (BHAUD, 1977). The variability in the number of stout setae and the asymmetry of the number of parapodia in the anterior region is a

Source : MNHN, Paris

peculiar feature of Grotta Sulfurea specimens. The cause of such a high morphological variability is unknown. However, enhanced levels of morphological variation have been reported for polychaetes from physically-stressed environments (ZUNARELLI VANDINI, 1971; COGNETTI, 1978).

Vent ecosystems are characterised by sharp temperature and salinity gradients and high concentrations of toxic compounds (CHILDRESS & FISHER, 1992). The occurrence of *P. socialis* population in this extreme environment suggests a high adaptive capability of this species. However, many marine polychaetes with wide ecological distribution have been demonstrated to be complexes of species (GRASSLE & GRASSLE, 1976; GUÉRIN & KERAMBRUN, 1984; ABBIATI, 1989). The same condition may be occurring in *P. socialis* as in these other species.

Further studies are in progress on the ecology and population genetics of *P. socialis*, and on the role of chemosynthesis in the trophic webs of the Grotta Sulfurea and other sulphurous caves at Capo Palinuro (ABBIATI *et al.*, 1992).

## ACKNOWLEDGMENTS

We thank Dr. E.C. SOUTHWARD and Dr C.N. BIANCHI for stimulating discussions and the helpful co-operation during the field work; Dr M.C. KENNICUTT and Dr J. ALCALA-HERRERA, Geochemical and Environmental Research Group, Texas A & M University, for the stable carbon isotope data; Dr M. ALVISI for his revision of the Grotta Sulfurea drawing. We also thank Mr. L. GHELIA, Mr. F. BARBIERI and the staff of the diving centre Pesciolino Sub for logistic support.

## REFERENCES

ABBIATI, M., 1989. — *Variabilità morfologica e genetica in nereidi (Annelida, Polychaeta) di habitat salmastri.* Doctoral Thesis, University of Genova, 194 pp.

ABBIATI, M., AIROLDI, L., ALVISI, M., BIANCHI, C.N., CINELLI, F., COLANTONI, P. & MORRI, C., 1992. — Preliminary observations on benthic communities in a submarine cave influenced by hydrothermal springs. *Rapp. Comm. int. Mer Medit.*, **33** : 25.

ALVISI, M., 1991. — Tecnica di rilevamento subacqueo. *In:* M. ABBIATI (ed.), *Lezioni del Corso Formativo per Ricercatore Scientifico Subacqueo.* ISSD Publisher, Italy : 13-28.

BELLAN, G., 1964. — Contribution à l'étude systématique, bionomique et écologique des Annélides Polychètes de la Méditerranée. *Recl Trav. Stn mar. Endoume*, **49** : 1-370.

BHAUD, M., 1974. — La campagne Hydroméde du N.O. Jean-Charcot. Première description de deux larves de Phyllochaetoptères (Annélides Polychètes). *Vie Milieu*, **24** : 453-470.

BHAUD, M., 1977. — Note sur quelques représentants du genre *Phyllochaetopterus* (Annélides Polychètes) et observations au microscope à balayage des soies spécialisées. *Vie Milieu*, **27** : 11-33.

BHAUD, M. & AMOUROUX, J.-M., 1975. — Signalisation nouvelle de *Phyllochaetopterus socialis* (Annélides Polychètes) à Banyuls-sur-Mer. *Vie Milieu*, **25** : 335-339.

CHILDRESS, J.J. & FISHER, C.R., 1992. — The biology of hydrothermal vent animals: physiology, biochemistry and autotrophic symbioses. *Oceanogr. mar. Biol. ann. Rev.*, **30** : 337-341.

CLAPARÈDE , E., 1868. — Les Annélides Chétopodes du Golfe de Naples. *Mém. Soc. Phys. Hist. nat. Genève*, **20** : 1-209.

CLINE, J.D., 1969. — Spectrophotometric determination of hydrogen sulphide in natural waters. *Limnol. Oceanogr.*, **14** : 454-458.

COGNETTI, G., 1978. — On some aspects of the ecology of benthic littoral Polychaetes. *Boll. Zool.*, **45** : 145-154.

DAY, J.H., 1967. — A monograph on the Polychaeta of Southern Africa. *Trust. Brit. Mus. (Nat. Hist. Publ.*, London : 1-878 pp.

DAY, J.H., 1973. — *New Polychaeta from Beaufort with a key to all species recorded from North Carolina.* NOAA Tech. Rep., NMFS Circ. 375, 141 pp.

Source : MNHN, Paris

DESBRUYERES, D., GAILL F., LAUBIER L. & FOUQUET Y., 1985. — Polychaetous annelids from hydrothermal vent ecosystems: an ecological overview. *Bull. biol. Soc. Wash.*, **6** : 103-116.

FAUVEL, P., 1927. — Polychètes sédentaires. *Faune Fr.*, **16** : 1-494.

FICHEZ, R., 1990. — Decrease in allochthonous organic inputs in dark submarine caves, connection with lowering in benthic community richness. *Hydrobiologia*, **207** : 61-69.

FICHEZ, R., 1991. — Benthic oxygen uptake and carbon cycling under aphotic and resource-limiting conditions in a submarine cave. *Mar. Biol.*, **110** : 137-143.

FISHER, C.R., 1990. — Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *C.R.C. Critical Rev. Aqu. Sci.*, **2** : 300-436.

GETTLESON, D.A., PHILLIPS, N.W. & HAMMER, R.M., 1985. — Dense polychaete (*Phyllochaetopterus socialis*) mats on the South Carolina continental shelf. *North. Gulf Sci.*, **7** : 167-170.

GIBBS, P.E., 1971. — The Polychaeta fauna of the Solomon Islands. *Bull. Br. Mus. (nat. Hist.)*, **21** : 101-211.

GRASSLE, J.F., 1985. — The ecology of deep-sea hydrothermal vent communities. *Adv. Mar. Biol.*, **23** : 301-362.

GRASSLE, J.F. & GRASSLE, J.P., 1976. — Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science*, **192** : 567-569.

GUÉRIN, J.P. & KERAMBRUN, P., 1984. Mise en évidence de deux types biochimiques au sein d'une population de *Malacoceros fuliginosus* (Annelida Polychaeta) de Méditerranée. *Bull. Soc. Zool. Fr.*, **109** : 347-351.

HARMELIN, J.G., VACELET, J. & VASSEUR, P., 1985. — Les grottes sous-marines obscures : un milieu extrême et un remarquable biotope refuge. *Téthis*, **11** : 214-229.

JANNASCH, H.W., 1985. — The chemosynthetic support of life and microbial diversity at deep sea hydrothermal vents. *Proc. Royal Soc.*, **225** : 277-297.

LAUBIER, L., 1966. — Le coralligène des Albères. Monographie biocénotique. Thèse Doc. ès Sci., Univ. Paris. *Annls Inst. océanogr. Monaco*, **43** : 137-316.

MCCARTY, D.M., 1974. — *The polychaetes of Seven and One-half Fathom Reef*. M.S. Thesis, Texas A & I Univ., Kingsville, 136 pp.

MUSCIO, G., 1985. — Il fenomeno carsico dell'area Camerota - Palinuro (Salerno, Campania). *Mondo Sotterraneo*, n.s., a. **9** : 13-42.

MUSCIO, G. & SELLO, U., 1989. — Le ricerche del Circolo Speleologico e Idrologico Friulano nell'area di Capo Palinuro. *Mondo Sotterraneo*, n.s., a. **13** : 41-72.

OTT, J.A. & SVOBODA, A., 1976. — Sea caves as model systems for energy flow studies in primary hard bottom communities. *Pubbl. Staz. Zool. Napoli*, **40** : 477-485.

REYSS, D., 1971. — Les canyons sous-marins de la mer Catalane : le rech du Cap et le rech Lacaze-Duthiers. III. Les peuplements de la macrofaune benthique. *Vie Milieu*, **22** : 529-613.

SOUTHWARD, A.J., 1989. — Animal communities fuelled by chemosynthesis: life at hydrothermal vents, cold seeps and in reducing sediments. *J. Zool., Lond.*, **217** : 705-709.

SOUTHWARD, E.C., 1987. — Contribution of symbiotic chemoautotrophs to the nutrition of benthic invertebrates. *In*: M. SLEIGH (ed) *Microbes in the sea*. Ellis Horwood, England : 83-118.

TARASOV, V.G., PROPP, M.V., PROPP, L.N., ZHIRMUNSKY, A.V., NAMSAREV, B.B., GORLENKO, V.M. & STARYNIN, D.A., 1990. — Shallow-water gasohydrothermal vents of Ushishir Volcano and the ecosystem of Kraternaya Bight (The Kurile Islands). P.S.Z.N.I : *Mar. Ecol.*, **11** : 1-23.

TUNNICLIFFE, V., 1991. — The biology of hydrothermal vents: ecology and evolution. *Ocean. mar. Biol. ann. Rev.*, **29** : 319-407.

ZUNARELLI VANDINI, R., 1971. — Observations on a population of *Podarke pallida* (Polychaete: Hesionidae) in heavily polluted waters. *Boll. Zool.*, **38** : 177-180.

Source : MNHN, Paris

Source : MNHN, Paris

# Contribution of the polychaetous annelids to the diet of some brazilian fishes

*A. Cecília Z. AMARAL*, Edmundo F. NONATO ** & Mônica A.V. PETTI***

* Depto. Zoologia, IB
Universidade Estadual de Campinas
CP. 6109, 13081-970 - Campinas, SP, Brazil
** Depto. Oceanografia Biologica, IO
Universidade de Sao Paulo
CP. 9075, 05508 - Sao Paulo, SP, Brazil

ABSTRACT

Otter trawls for fish were taken between the three offshore islands, Anchieta, Vitória and Couves off the southeast coast of Brazil in order to determine their food habits. The stomachs of 2834 specimens of fish belonging to 77 species were examined; 1076 were found to be empty and 595 contained polychaetes. Sixty-five species of polychaetes were identified, with the most frequent ones belonging to the genera *Notomastus, Onuphis, Anaitides, Pherusa, Laonice, Diopatra* and *Euclymene*. The polychaete families were grouped according to their habitat, that is, the bottom, in subsurface sessile, subsurface mobile, surface sessile and surface mobile. The subsurface mobiles had the highest percentage (42.8 %) in the stomach contents with food present.

RÉSUMÉ

**Le rôle des annélides polychètes dans le régime alimentaire de certains poissons brésiliens**

Dans le but d'estimer la part des polychètes dans le régime alimentaire des poissons benthiques et "démersaux" de la côte Sud-Est du Brésil, une série de prélèvements a été réalisée à l'aide d'un chalut à panneaux du type "otter trawl" dans la région comprise entre les îles Anchieta, Vitória et Couves à des profondeurs comprises entre 10 et 50 m. Le contenu stomacal de 2834 individus de poissons appartenant à 77 espèces a été examiné : 1076 estomacs étaient vides et 595, soit 33,8 % des autres, contenaient des polychètes. Environ 65 espèces de polychètes ont été identifiées, les plus fréquentes appartenant, par ordre décroissant d'importance numérique, aux genres *Notomastus, Onuphis, Anaitides, Pherusa, Laonice, Diopatra* et *Euclymene*. Les familles de Polychètes ont été groupées suivant la position qu'elles occupent sur le fond, soit : sub-surface sessile, sub-surface mobile, surface sessile et surface mobile. Les sub-surfaces mobiles sont les plus fréquentes (42,8 %) dans le contenu des estomacs examinés.

---

AMARAL, A.C.Z., NONATO, E.F. & M.A.V. PETTI, 1994. — Contribution of the polychaetous annelids to the diet of some brazilian fishes. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 331-337. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

The role of polychaetes as food for fish has been limited to such authors as KAWAKAMI & AMARAL (1976, 1983), AMARAL & MIGOTTO (1980), BEN-ELIAHU, GOLANI & BEN-TUVIA (1983), BADALAMONTI & RIGGIO (1989) and BEN-ELIAHU & GOLANI (1990). Their objective was to determine the position polychaetes occupy among the prey eaten by fish.

Since earlier studies off the coast of Brazil had indicated a high incidence of polychaetes as food for fish, our primary objective was to determine in greater detail their role as a major food element. We also attempted to clarify those factors conditioning the apparent selectivity of certain species of fish when catching food as related to the ecological position occupied by the polychaetes.

## STUDY AREA

The samples were taken from the northern coast of the State of São Paulo between the islands of Anchieta, Vitória and Couves (23°31' - 23°45' S and 44°58' - 45°06' W, Fig. 1) from 10 to 50 m in depth. The bottom sediments consist of sandy mud with occasional patches of sand or shell fragments near the islands. Off Vitória Island in 40 and 50 m depth the sediment is muddy with sporadic presence of lime plates. Throughout the area low temperature water (<18 °C) (the so called South Atlantic Central Water - SACA) occurs near the bottom during the summer months (CASTRO FILHO *et al.*, 1987).

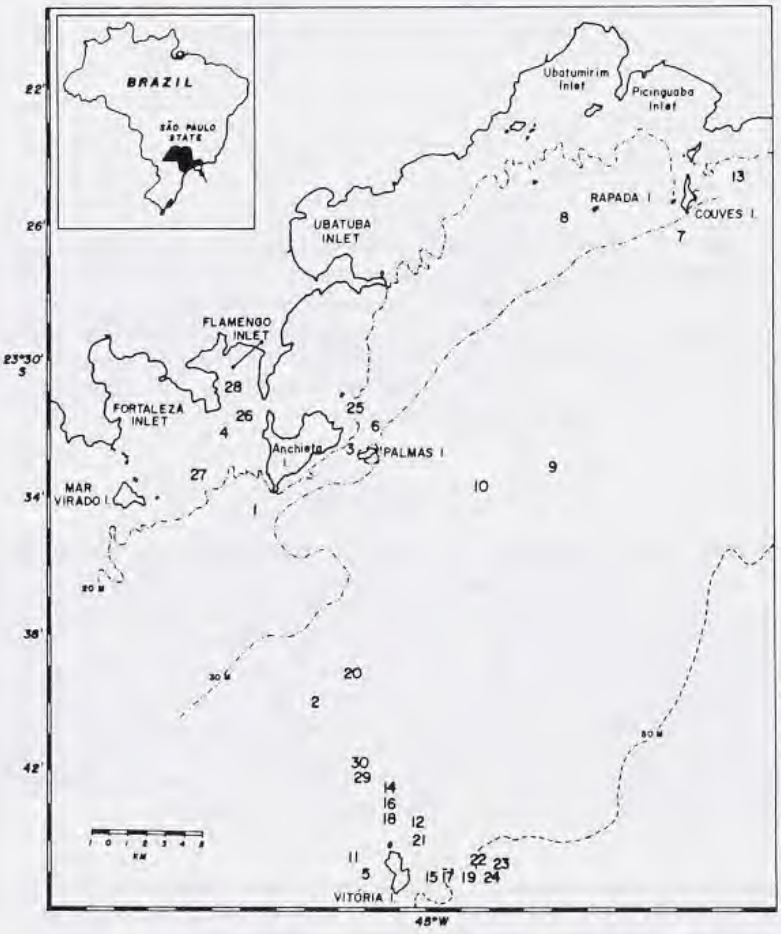



FIG. 1. — Location of catches between the islands Anchieta, Vitória and Couves.

Source : MNHN, Paris

## MATERIAL AND METHODS

The samples comprised 30 trawl net hauls taken August 1978 through May 1979 and September 1982 through May 1985. The organisms caught in the net were sorted and packed on ice for future analyses of the digestive tract. Seventy percent of the specimens of the more abundant species were kept; whereas, all specimens were retained for those species with fewer numbers. In the laboratory the stomachs were removed and preserved individually with 10 % formaldehyde. The contents of each fish was analyzed individually under a dissecting microscope, and the food items recorded.

The polychaetes were separated and identified to the lowest possible taxon. The numerical frequency was used to analyze the results, each fragment possessing a head was counted. The polychaetes were grouped according to life habits, following the criteria proposed by FAUCHALD & JUMARS (1979) and GASTON (1987).

The families of polychaetes were distributed into four groups on the basis of their spatial location on the substrate or mobility as subsurface sessile, subsurface mobile, surface sessile and surface mobile.

## RESULTS AND DISCUSSION

Of the 2834 stomachs examined from 77 species of fish, 1076 (38 %) were empty and not included in further analyses. A total of 1398 polychaetes were encountered from 595 fishes (34 %) of which 1134 could be identified at least family.

The examination of the Polychaeta present in the stomachs of the fish permitted the identification of 28 families, 42 genera and 65 species (Table 1). Those species which were numerically the most abundant are indicated with an asterisk in Table 1.

TABLE 1. — Polychaete occurrence, number of individuals and numerical frequency found on stomach contents of demersal and benthic fishes.

| Species | #occur. | #inds. | Num. freq.(%) | Species | #occur. | #inds. | Num. freq.(%) |
|---|---|---|---|---|---|---|---|
| ONUPHIDAE | 10 | 225 | 19.8 | GONIADIDAE | 130 | 20 | 1.8 |
| *Diopatra* sp. | 6 | 7 | 0.6 | *Glycinde* sp. | 3 | 6 | 0.5 |
| **Diopatra cuprea* | 3 | 5 | 0.4 | *Glycinde multidens* | 6 | 1 | 1.2 |
| **Diopatra spiribranchis* | 5 | 57 | 5.0 | *Goniada maculata* | 1 | 19 | 0.1 |
| *Diopatra splendidissima* | 11 | 22 | 1.9 | EUNICIDAE | 18 | 3 | 1.7 |
| *Diopatra tridentata* | 1 | 2 | 0.2 | *Eunice* sp. | 2 | 16 | 0.3 |
| *Mooreonuphis* sp. | 1 | 2 | 0.2 | Unidentified | 16 | 19 | 1.4 |
| *Mooreonuphis fragilis* | 2 | 6 | 0.5 | AMPHARETIDAE | 13 | 7 | 1.7 |
| **Mooreonuphis nebulosa* | 8 | 15 | 1.3 | *Amphicteis sp.* | 4 | 2 | 0.6 |
| *Mooreonuphis stigmatis* | 2 | 5 | 0.4 | *Amphicteis latibranchiata* | 1 | 6 | 0.2 |
| *Onuphis* sp. | 31 | 36 | 3.2 | *Isolda pulchella* | 4 | 4 | 0.5 |
| *Onuphis eremita* | 5 | 11 | 1.0 | Unidentified | 4 | 14 | 0.4 |
| *Onuphis vexillaria* | 1 | 3 | 0.3 | LUMBRINERIDAE | 9 | 3 | 1.2 |
| Unidentified | 54 | 54 | 4.8 | *Lumbrineris* sp. | 2 | 10 | 0.3 |
| CAPITELLIDAE | 102 | 222 | *19.6* | *Lumbrineris tetraura* | 6 | 1 | 0.9 |
| *Notomastus* sp. | 10 | 17 | 1.5 | Unidentified | 1 | 14 | 0.1 |
| *Notomastus lobatus* | 88 | 201 | 17.7 | SIGALIONIDAE | 8 | 3 | 1.2 |
| Unidentified | 4 | 4 | 0.4 | *Sthenelais* sp. | 2 | 6 | 0.3 |
| CIRRATULIDAE | 13 | 105 | 9.3 | *Sthenelais oculata* | 3 | 2 | 0.5 |
| *Audouinia tentaculata* | 3 | 5 | 0.4 | *Thalenessa lewisii* | 1 | 3 | 0.2 |
| **Cirratulus filiformis* | 5 | 94 | 8.3 | Unidentified | 2 | 14 | 0.3 |
| Unidentified | 5 | 6 | 0.5 | TRICHOBRANCHIDAE | 5 | 8 | 1.2 |
| MALDANIDAE | 80 | 97 | 8.6 | *Terebellides* sp. | 3 | 4 | 0.7 |
| *Euclymene* sp. | 6 | 12 | 1.1 | *Terebellides anguicomus* | 1 | 2 | 0.4 |

Source : MNHN, Paris

TABLE 1 (continued). — Polychaete occurrence, number of individuals and numerical frequency found on stomach contents of demersal and benthic fishes.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Euclymene dalesi* | 7 | 16 | 1.4 | *Terebellides stroemi* | 1 | 12 | 0.2 |
| Unidentified | 67 | 69 | 6.1 | PILARGIDAE | 8 | 11 | 1.1 |
| OPHELIIDAE | 18 | 89 | 7.9 | *Loandalia americana* | 7 | 1 | 0.1 |
| *Ammotrypane aulogaster* | 5 | 57 | 5.0 | *Sigambra grubii* | 1 | 9 | 0.1 |
| *Armandia* sp. | 1 | 1 | 0.1 | NEPHTYDAE | 6 | 7 | 0.8 |
| *Armandia agilis* | 6 | 18 | 1.6 | *Nephtys* sp. | 5 | 2 | 0.6 |
| *Travisia forbesii* | 6 | 13 | 1.2 | *Nephtys paradoxa* | 1 | 8 | 0.2 |
| TEREBELLIDAE | 42 | 62 | 5.8 | AMPHINOMIDAE | 6 | 4 | 0.7 |
| *Artacama benedeni* | 4 | 10 | 0.9 | *Pseudeurythoe* sp. | 2 | 4 | 0.4 |
| *Loimia medusa* | 3 | 4 | 0.4 | Unidentified | 4 | 7 | 0.4 |
| *Pista* sp. | 2 | 2 | 0.2 | ORBINIIDAE | 5 | 4 | 0.6 |
| *Streblosoma bairdi* | 6 | 14 | 1.2 | *Naineris setosa* | 2 | 3 | 0.4 |
| *Thelepus* sp. | 2 | 4 | 0.4 | Unidentified | 3 | 5 | 0.3 |
| *Thelepus setosus* | 6 | 9 | 0.8 | NEREIDAE | 3 | 1 | 0.4 |
| Unidentified | 19 | 19 | 1.7 | *Neanthes bruaca* | 1 | 4 | 0.1 |
| FLABELLIGERIDAE | 38 | 59 | 5.2 | Unidentified | 2 | 4 | 0.4 |
| *Pherusa laevis* | 17 | 27 | 2.4 | SABELLIDAE | 3 | 1 | 0.4 |
| *Pherusa parmata* | 8 | 17 | 1.5 | *Chone* sp. | 1 | 3 | 0.1 |
| *Piromis arenosus* | 5 | 7 | 0.6 | Unidentified | 2 | 4 | 0.3 |
| Unidentified | 8 | 8 | 0.7 | DORVILLEIDAE | 2 | 4 | 0.4 |
| SPIONIDAE | 24 | 44 | 3.9 | *Dorvillea rudolphi* | 2 | 4 | 0.4 |
| *Laonice branchiata* | 13 | 31 | 2.7 | MAGELONIDAE | 2 | 4 | 0.4 |
| *Paraprionospio pinnata* | 1 | 3 | 0.3 | *Magelona nonatoi* | 2 | 4 | 0.4 |
| Unidentified | 10 | 10 | 0.9 | EUPHROSINIDAE | 1 | 4 | 0.4 |
| PHYLLODOCIDAE | 21 | 43 | 3.8 | *Euphrosine* sp. | 1 | 3 | 0.4 |
| *Anaitides* sp. | 1 | 2 | 0.2 | HESIONIDAE | 2 | 3 | 0.3 |
| *Anaitides tamoya* | 20 | 41 | 3.6 | Unidentified | 2 | 2 | 0.3 |
| GLYCERIDAE | 14 | 25 | 2.2 | PECTINARIIDAE | 1 | 2 | 0.2 |
| *Glycera* sp. | 2 | 2 | 0.2 | *Pectinaria laelia* | 1 | 1 | 0.2 |
| *Glycera americana* | 7 | 15 | 1.3 | POLYNOIDAE | 1 | 1 | 0.1 |
| *Hemipodus rotundus* | 1 | 4 | 0.4 | Unidentified | 1 | 1 | 0.1 |
| Unidentified | 4 | 4 | 0.4 | | | | |

* Indicates most frequently occurring polychaetes in the stomach of fish.

Table 2 lists the 10 most frequently caught species of fish with the number of stomachs containing food in their stomach and the percent occurrence of polychaetes.

The feeding habits of the 10 species listed in Table 2 characterize as benthic feeders and fed specially on crustaceans, polychaetes, ophiuroids, molluscs and fish. Polychaetes were present in 38.5 % to 88.0 % of the stomachs analyzed.

Other fish, among which *Dasyatis americana* HILDEBRAND & SCHROEDER, 1828 and *Narcine brasiliensis* (OLFERS, 1831), fed upon polychaetes regularly but were not included herein due to the small number collected.

The above results confirm the observations of KAWAKAMI & AMARAL (1983), who showed that up to 86.0 % of the total volume of organisms present in the stomach of two species of flat-fishes, *Etropus longimanus* and *Symphurus jenynsi* were polychaetes. AMARAL & MIGOTTO (1980) also observed a high incidence of polychaetes in the stomachs of *Paralonchurus brasiliensis* (77.3 %), *Micropogonias furnieri* (68.5 %) and *Orthopristis ruber* (39.9 %) in Ubatuba region of Brazil.

The grouping of polychaete families as a function of habits constitutes an effective way to clarify why they are preferred by certain fishes. As discussed by CHAO & MUSIK (1977) for young Sciaenidae, the search for food

Source : MNHN, Paris

TABLE 2. — List of the most frequently caught fish species, number of stomachs with food and percent occurrence of polychaetes in the stomach contents.

| Species | Stomach with contents | Frequence polychaete |
|---|---|---|
| RHINOBATIDAE | | |
| *Zapteryx brevirostris* (Muller & Henle, 1941) | 41 | 56.1 % |
| ARIIDAE | | |
| *Genidens genidens* (Valenciennes, 1839) | 24 | 87.5 % |
| SERRANIDAE | | |
| *Dules auriga* Cuvier, 1829 | 26 | 38.5 % |
| GERREIDAE | | |
| *Eucinostomus gula* (Cuvier, 1830) | 22 | 63.6 % |
| POMADASYIDAE | | |
| *Conodon nobilis* (Linnaeus, 1758) | 39 | 53.8 % |
| *Orthopristis ruber* (Cuvier, 1830) | 38 | 57.9 % |
| SCIANIDAE | | |
| *Micropogonias furnieri* (Desmarest, 1823) | 108 | 73.1 % |
| *Paralonchurus brasiliensis* (Steindachner, 1815) | 336 | 71.7 % |
| *Umbrina canosai* Berg, 1895 | 68 | 42.6 % |
| BOTHIDAE | | |
| *Etropus crossotus* Jordan & Gilbert, 1891 | 27 | 51.9 % |

depends more on the habits of the prey than on selective preference. We grouped the families of polychaeta in accordance to the position they occupy in the bottom and their presumed ability to escape the predator. The polychaete families were distributed in four groups as indicated in Table 3.

TABLE 3. — Polychaete families distributed according to the position they occupy in the sediment.

| 1. SUB-SURFACE SESSILE | 3. SURFACE SESSILE |
|---|---|
| Flabelligeridae | Ampharetidae |
| Mageloniidae | Cirratulidae |
| Maldanidae | Sabellidae |
| Pectinariidae | Terebellidae |
| | Trichobranchidae |
| 2. SUB-SURFACE MOBILE | 4. SURFACE MOBILE |
| Capitellidae | Amphinomidae |
| Glyceridae | Eunicidae |
| Goniadidae | Dorvilleidae |
| Lumbrineridae | Euphrosinidae |
| Nephyidae | Hesionidae |
| Orbiniidae | Onuphidae |
| Phyllodocidae | Polynoidae |
| Pilargidae | Sigalionidae |
| Spionidae | |

The 10 most frequently caught fish species were placed into three groups on the basis of their feeding behaviour (Fig. 2). One group of species feed mainly on subsurface mobile polychaetes; these were: *Eucinostomus gula, Genidens genidens, Micropogonias furnieri, Zapteryx brevirostris* and *Umbrina canosai*. A second fed on subsurface mobile ones; these were: *Etropus crossotus* and *Conodon nobilis*. The third group

Source : MNHN, Paris

FIG. 2. — Species of fish grouped in function of preferences on polychaetes position and mobility. A, those eating mainly surface mobile forms. B, those feeding on subsurface mobile ones. C, those revealing no definite preference.

showed no defined preferential habit to the position on the substrate or mobility of the polychaetes they caught; these were: *Orthopristis ruber, Paralonchurus brasiliensis* and *Dules auriga.*

The results of the study on the distribution of the polychaetes in the same area carried out by MORGADO (1988), when analyzed under the same criterion, showed values very similar to those corresponding to the stomach contents.

This comparison between the polychaetes found in the area and the polychaetes ingested indicates that these animals are being preyed upon by members of the fish community in accordance to their availability. However, when one analyses the data species by species, it becomes obvious that the preference for one or another group of polychaetes by a determined species of fish can occur. This indicates the influence of other factors, such as morphological adaptations or the capacity to explore the substract in a different way.

The group of fish which feed mainly on subsurface mobile polychaetes have the capacity to churn up the sediment in the search for food and frequently uses this manner to capture their prey. On the other hand, *Etropus*

Source : MNHN, Paris

*crossatus* and *Conodon nobilis* present certain limitations concerning this capacity, restricting themselves more to the capture of a group less available in the environment, the surface mobiles.

| CATEGORIES | POLYCHAETES | |
|---|---|---|
| | in the area (MORGADO, 1988) | in the stomach analysis |
| Surface mobile | 27.7 % | 25.0 % |
| Surface sessile | 15.1 % | 18.0 % |
| Sub-surface mobile | 42.0 % | 42.8 % |
| Sub-surface sessile | 15.3 % | 14.3 % |

The criterion of accessibility herein adapted may contribute to a better evaluation of the role of polychaetes as more frequent or preferential prey of different marine organisms, and also to clarify the existence of specific food selection processes on the part of their habitual predators.

## ACKNOWLEDGEMENTS

We are particularly indebted to the Instituto Oceanográfico (IO-USP) for the logistics support. Special thanks should be given to Dr. Claudia ALVES MAGALHÃES and Jacques VIELLIARD for their suggestions. We are also grateful to Dr. Donald REISH and two anonymous reviewers who improved earlier versions of this work. This research was supported by funds from the "Conselho Nacional de Pesquisa (CNPq)", "Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP)" and "Comissão Interministerial de Recursos do Mar (CIRM)".

## REFERENCES

AMARAL, A.C.Z. & MIGOTTO, A.E., 1980. — Importância dos anelídeos poliquetas na alimentação da macrofauna demersal e epibentônica da região de Ubatuba. *Bolm Inst. oceanogr., S. Paulo*, **29** : 31-35.

BADALAMENTI, F. & RIGGIO, S., 1989. — I policheti dei contenuti stomacali di *Mullus surmuletus* L. (Pisces: Mullidae) nel Golfo di Palermo. *Oebalia*, **15** : 79-87.

BEN-ELIAHU, M.N. & GOLANI, D., 1990. — Polychaete annelids on gut content of goat fish (Mullidae) with new polychaete records. Mediterranean coast and the Gulf of Eilat (Red Sea). *Mar. Ecol.* **11** : 193-205.

BEN-ELIAHU, M.N., GOLANI, D. & BEN-TUVIA, A., 1983. — On predation on polychaetes (Annelids) by the squirrelfish *Adioryx ruber* (Holocentridae), with a new polychaete record for the mediterranean coast of Israel. *Tethys*, **11** : 15-19.

CASTRO FILHO, B.M., MIRANDA, L.B. & MIYAO, S.Y., 1987. — Condições hidrográficas da plataforma continental ao longo de Ubatuba : Variações Sazonais em média escala. *Bolm Inst. oceanogr., S. Paulo*, **35** : 135-151.

CHAO, L.N. & MUSIK, J.A., 1977. - Life history, feeding habits and functional morphology of juvenile Scianidae fishes in the York River estuary, Virginia. *Fish. Bull.*, **75** : 657-702.

FAUCHALD, K. & JUMARS, P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Ann. Rev. Oceanogr. mar. Biol.*, **17** : 193-284.

GASTON, G.R., 1987. — Benthic polychaeta of the middle Atlantic Bight: feeding and distribution. *Mar. Ecol. Prog. Ser.*, **36** : 251-262.

KAWAKAMI, E. & AMARAL, A.C.Z., 1976. — Importância dos anelídeos poliquetas no regime alimentar de alguns pleuronectiformes. *Supl. Ciênc. Cult., S. Paulo*, **28** : 420.

KAWAKAMI, E. & AMARAL, A.C.Z., 1983. — Importância dos anelídeos poliquetas no regime alimentar de *Etropus longimanus* Norman, 1983 e *Symphurus jenynsi* Evermann Kendall, 1902 (Pisces, Pleuronectiformes) *Iheringia, Sér. Zool., Porto Alegre*, **62** : 47-54.

MORGADO, E.H., 1988. — *Anelídeos Poliquetos do Sublitoral da Região de Ubatuba - SP, compreendida entre as Ilhas Anchieta e Vitória*. Tese de Doutorado, Universidade Estadual de Campinas, Instituto de Biologia, 181pp.

Source : MNHN, Paris

Source : MNHN, Paris

# Ecology of *Pherusa* sp. (Polychaeta, Flabelligeridae)

*Analía AMOR*

Instituto de Embriología, Biología e Histología, Facultad de Ciencias Médicas
Universidad Nacional de La Plata (CONICET), calle 60 y 120
1900 La Plata, Argentina

ABSTRACT

*Pherusa sp.* is an endolithic species which burrows into hard substrates (loess) with a range of cohesion from 0 to 254.6 kg. $cm^{-2}$. The burrow is a tube which is closed posteriorly. The shape of the tube reflects in saggital section the position of the animal inside it. The wall of the burrow is lined with aragonite. The lining is thickest near the opening of the tube. A dorsal shield on the first 3 chaetigers function as a lid to the burrow when the animal is withdrawn. During feeding the two palps and the branchiae play a very important role. The food reaches the mouth by different prostomial ciliary grooves. As with many other boring marine animals, *Pherusa* sp. is a microphaga and detritous feeder. Waste products and gametes are discharged to the sea through the two nephridiopores located in the head near the inner line of branchiae. The first 36 segments of the body are longer and thicker than the rest which resembles a tail. The anus is located on the terminal end of the tail which is reflexed, making the body U-shaped. The mouth is ventral with respect to the anus. The intertidal population studied inhabits a loess which on the exposed surface presents a large and dense stratum of coralline algae. Endolithic species such as *Polydora* sp., *Themiste petricola, Lithophaga patagonica,* etc., surround the holes of *Pherusa sp.* The density of the species in the intertidal loess of Santa Elena, province of Buenos Aires, Argentina was 14 specimens in a quadrant of 100 $cm^2$. The species shows indirect development and some of its larval stages can be collected by washing the epilithic coralline algae from November to February. *Pherusa sp.* shows characteristics of tubicolous animals. The gradient of cohesion (0 to 254.6 kg. $cm^{-2}$) suggests that this species possesses a physical as well as chemical mechanism for burrowing. The presence of acid mucopolysaccharides in the tegument gland secretion confirms this deduction. The lining of the tube, thicker around the aperture could indicate a function of consolidation of the burrow in substrates of low cohesion, but this thickening was also present in high cohesion substrates. The aragonite lining deposited by *Pherusa sp.* on the burrow walls contributes to loess particles cementation and rock hardness increase.

RÉSUMÉ

**Écologie de *Pherusa* sp. (Polychaeta, Flabelligeridae)**

*Pherusa* sp. est une espèce endolithique qui perfore les substrats durs (loess). La perforation consiste en un tube fermé dans la partie postérieure dont la forme, en section sagittale, indique la position de l'animal à l'intérieur du tube. La paroi du tube est couverte d'aragonite dont l'épaisseur augmente autour de l'ouverture du tube. Une plaque dorsale sur les trois premiers segments de l'animal ferme l'ouverture du tube lorsque l'animal se rétracte. Pendant l'alimentation, les deux palpes et les branchies jouent un rôle très important. Les aliments arrivent à la bouche par plusieurs sillons ciliés

AMOR, A., 1994. — Ecology of *Pherusa* sp. (Polychaeta, Flabelligeridae) *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 339-346. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

du prostomium. Comme beaucoup d'animaux marins sédentaires, *Pherusa* sp. est microphage et mangeur de détritus. Les déchets et les gamètes sont libérés dans la mer par les néphridiopores situés dans la tête, près de la ligne interne des branchies. Les 36 premiers segments du corps du ver sont plus longs, plus larges et plus hauts que les autres lesquels réssemblent d'ailleurs à une queue. L'anus se trouve postérieurement, il se replie sur le corps formant un "u". Il en résulte que la bouche est ventrale par rapport à l'anus. La population intertidale étudiée habite un loess qui présente, sur la surface exposée, une strate dense et peuplée d'algues corallines. Des espèces endolithiques comme *Polydora* sp., *Themiste petricola, Lithophaga patagonica,* etc., entourent les trous de *Pherusa* sp. La densité de l'espèce à Santa Elena (Argentine) atteint 14 spécimens dans un carré de 10x10 cm L'espèce étudiée montre un développement indirect et quelques stades larvaires peuvent être recueillis en lavant les algues corallines epilithiques de novembre à février. *Pherusa* sp. présente les caractéristiques des animaux tubicoles. Le gradient de cohésion (0-254,6 kg. $cm^{-2}$) suggère que cette espèce possède un mécanisme physique et un autre chimique pour perforer les substrats durs. La présence de mucopolysaccharides acides dans la sécrétion des glandes du tégument conforte cette déduction.

## INTRODUCTION

The first objective of the "Bioturbations of the Buenos Aires Loess" program initiated in 1987, was to establish the relationship between the endolithic macrofauna and the characteristics of the hard substrate (AMOR *et al*, 1991). The second goal was to determine the role of the endolithic fauna in the deterioration of the intertidal loess of Santa Elena beach in the province of Buenos Aires, Argentina. The results of this study on the ecology of *Pherusa* sp. contribute to the knowledge of how *Pherusa* sp. leads to deterioration of the loess.

## MATERIALS AND METHODS

The adults of *Pherusa* sp. are endolithic and were collected during low tide on the rocky beach of Santa Elena (37°56'02" S; 58°11'35" W) in the province of Buenos Aires, Argentina.

The shoal consists of a bank 5 m high with a shelf with drainage channels (Fig. 1a). Tubes were found on the sides of small pools located within coralline algae at the mid-tide level (Fig. 1b). Rock samples were collected using a hammer and chisel and transported to the laboratory in buckets of seawater. In the laboratory the sanples were divided according to the study objectives: a) Direct observation of the worms within the rock in order to study their feeding behaviour. The samples were placed in plastic boxes containing sea-water of 32 P.S.U. salinity and kept at 24 °C which was similar to the environmental conditions. The worms were fed microscopic algae from cultures. Observations on feeding behaviour were made under a stereomicroscope. b) Adults were separated from their tubes and fixed with neutral 10 % formalin for staining with Alcian blue (MARTOJA & MARTOJA, 1967). c) The heads of a group of animals were fixed in Bouin's fluid, stained with Ehrlich's hematoxylene-eosin, and cut into sections 5 µm thick. d) The anterior region of the body was fixed in 2.5 % glutaraldehyde in Millonig's phosphate buffer adjusted to 970 milliomsmoles for scanning electron microscopic examination. Following dehydration in alcohol and acetone, the material was dried in liquid carbon dioxide in a critical point drier, coated with gold palladium and observed in a JEOL microscope. e) Fractions of the tube lining were separated from the rock and their mineral composition was determined using a Philips DRX x-ray diffractometer model PW 1011/00 with a copper tube, wavelength 1.5454 A, 18 A, 40 kV, goniometer velocity 2°. $min^{-1}$, paper speed 1200 mm. $h^{-1}$.

The pH of the seawater occupying the space between the animal and the wall of the tube was determined using "pHYDRION" pH test papers of two ranges: 0-13 and 3-5.5.

The population density was estimated by sampling at low tide using a systematic sampling plan (KRUMBAIN & GRAYBILL, 1965) which consisted of tracing seven transects perpendicular to the coastline, designated A, AB, BA, B, BC, CB, and C. Transects A, B, and C extended from the top of the bank to the sea. AB, BA, BC, and CB ran from the upper inhabited level of the beach to the sea (Fig. 4c).

The study area was 132 m wide (distance between A and C), the bank 5 m high (levels 1, 2 and 3), the beach 36 m long (from the base of the bank to the sea), and the sampled beach 6 m long (levels 4 and 5). The high tide reaches the bank at level 3. A square frame (10 x 10 cm) was used to count holes with animals at levels 4 and 5.

Source : MNHN, Paris

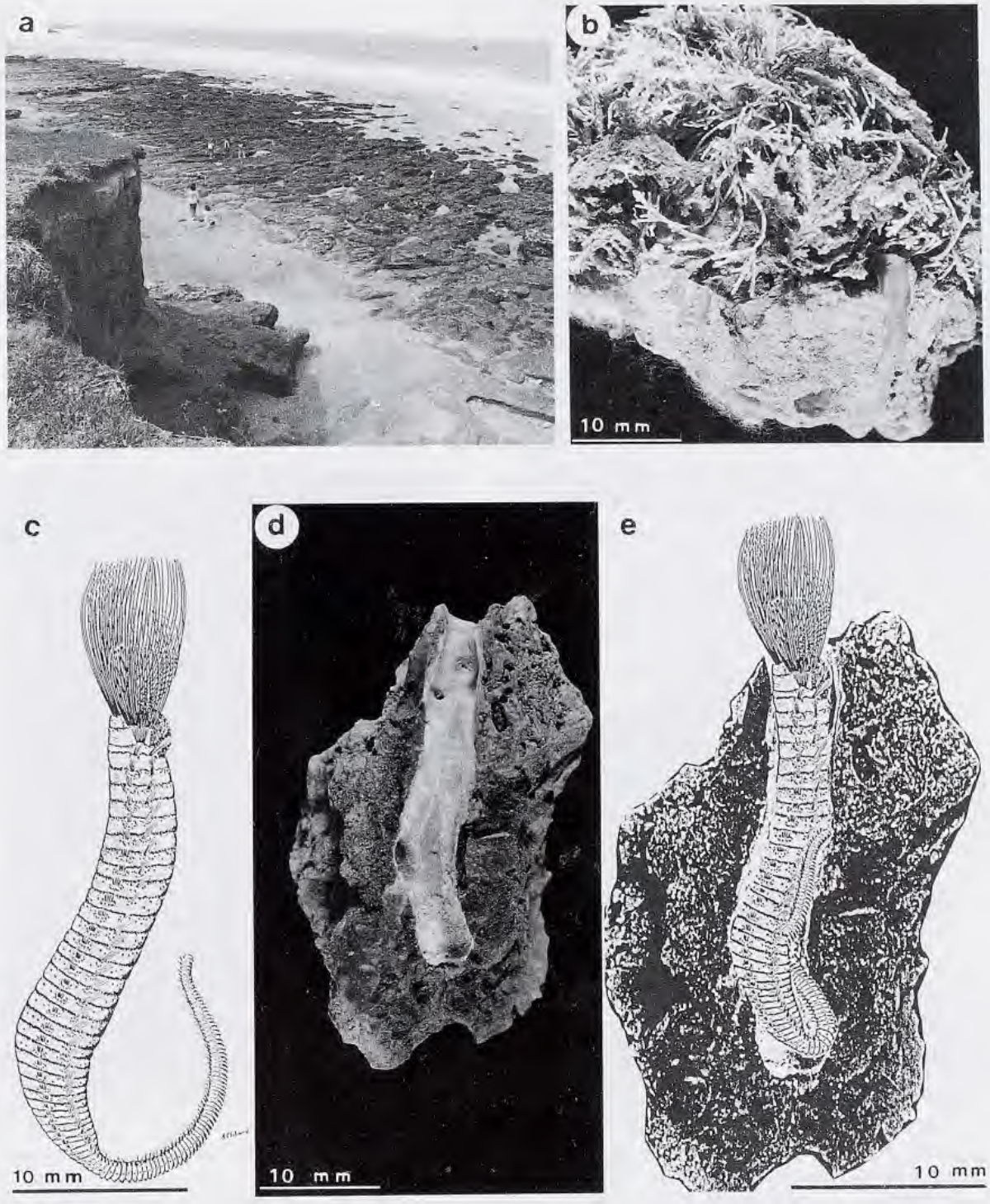



FIG. 1. — *Pherusa* sp.: **a**, general view of the collection area on Santa Elena beach. **b**, view of a rocky sample in the intertidal coralline algae zone with burrows. **c**, lateral view of the worm (drawing). **d**, burrow. **e**, burrow with worm inside it (composed).

Source : MNHN, Paris

## RESULTS

*Pherusa* sp. is an endolithic worm which burrows in hard substrates (Fig. 1c). The substrate in the sampling zone has been described as a loess which is continuously eroded by the sea (AMOR *et al.*,1991). The cohesion of the loess was found to range from 0 to 254.6 kg. $cm^{-2}$ in its resistance to compression. *Pherusa* sp. is found in loess throughout this range of resistances along with other species such as *Themiste petricola, Polydora* sp., *Lithophaga patagonica, Petricola patagonica* and *Saxicava solida.* This suggests that *Pherusa* sp. and the other species possess a chemical mechanism in addition to a physical mechanism, which permits them to burrow into highly cohesive rock (254.6 kg. $cm^{-2}$). Preliminary studies indicate that the glands of the tegument of *Pherusa* sp. secreted acid mucopolysaccharides as shown by the Alcian blue technique.

The burrow of *Pherusa* sp. is a blind-ended tube measuring up to 3 cm in length (Fig. 1d). Sagital cut of the tube indicates the position occupied by the animal. The tube walls are covered with aragonite (Fig. 2). The lining is thicker near the opening than elsewhere in the tube. A dorsal shield on the first 3 chaetigers function as a lid to the burrow when the animal is withdrawn. The seawater lying between the animal and the burrow has a pH of 5.

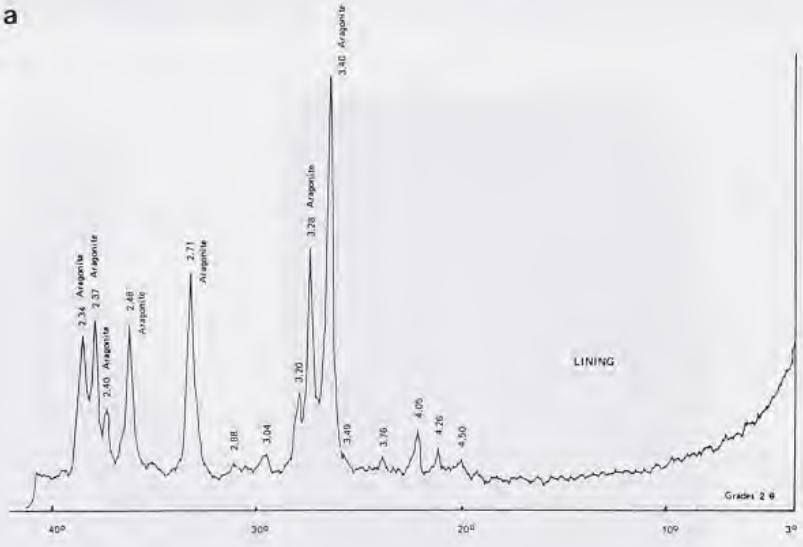



FIG. 2. — *Pherusa* sp.: **a**, diffractogram of the burrow lining.

The structures of the head and the chaetae which participate in feeding are described according to their functional role.

The head of *Pherusa* sp. can be either introverted or extended. It is usually found withdrawn into a chamber formed by a membrane extended in front of the first chaetiger. When the head is introverted, the membrane invaginates with it. The head is protruded followed by the chaetal cage during feeding. The chaetae of the first three segments of the body form the chaetal cage. The length of the chaetae decreases from the first to the third segment, and they are all oriented anteriorly (Fig. 3c). During feeding the chaetae are separated and moved backwards forming a filtering system.

The prostomium consists of the prostomial lobe with four eyes in the base, the ciliary grooves, a solid ridge between the right and the left ciliary grooves, the nuchal organs, the dorsal lip, the two palps and the two pads. The two prostomial tracts of cilia originate at the base of the two dorsal branchiae (Fig. 3a,b and d; Fig. 4a). The ciliated grooves flank the solid medial ridge up and surround the prostomial lobe. These grooves are prolonged as far as the ciliated fossae of the nuchal organs. The ciliated grooves continue to the base of the palps, cross over the pad to each side of the dorsal lip to the mouth. The palps originate in the ventral border of the prostomial lobe.

Source : MNHN, Paris

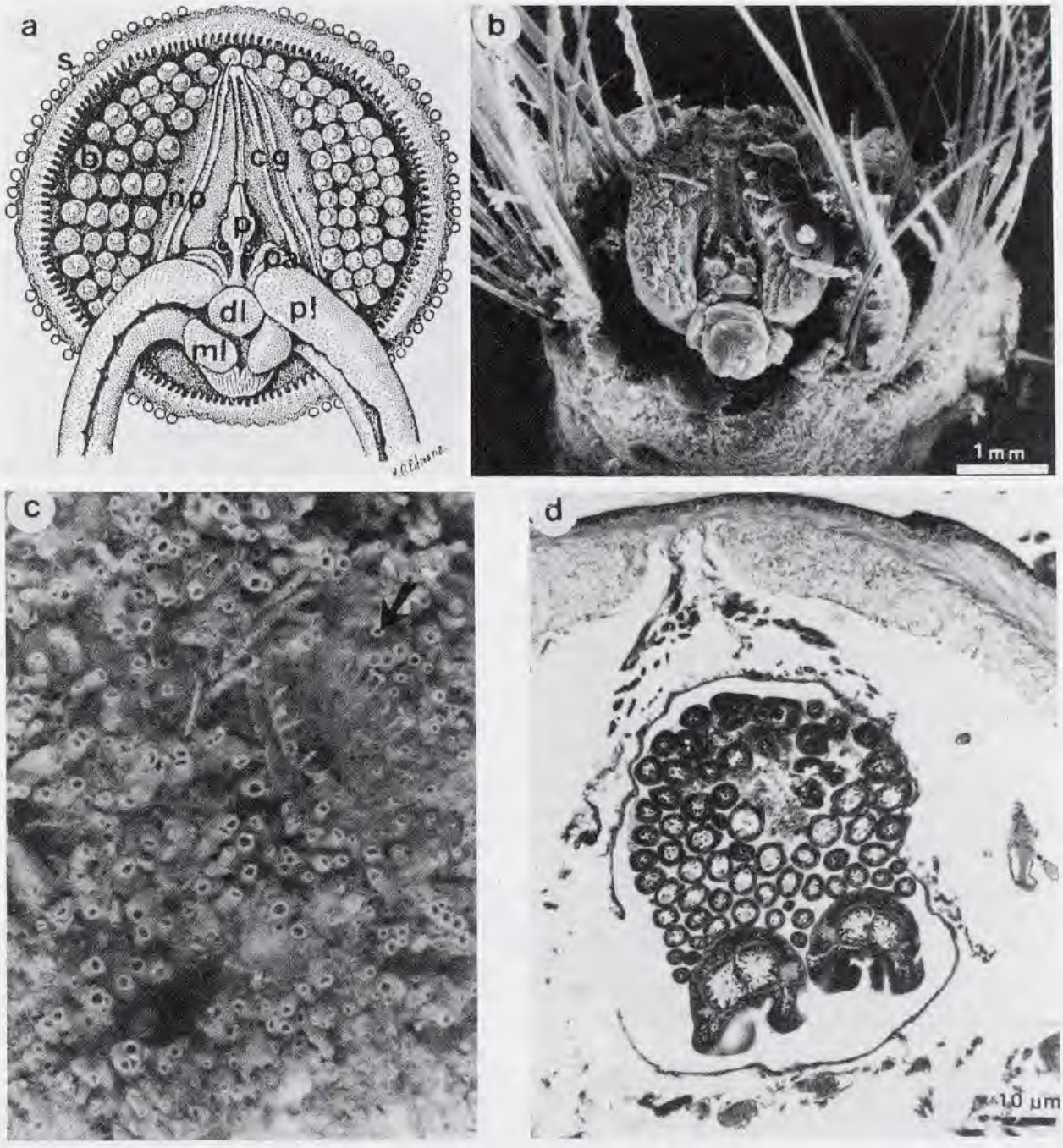



FIG. 3. — *Pherusa* sp.: **a**, schematic frontal view of head; P, prostomium; PL, palp; DL, dorsal lip; CG, ciliary groove; NP, nephridiopore; ML, median lip; S, chaeta. **b**, head evaginated with the buccal capsule extruded (palps cut). **c**, the chaetae of the first three segments are separated like fans in this worm shown on the rock. **d**, branchiae impel food particles to the ciliary grooves.

Source : MNHN, Paris

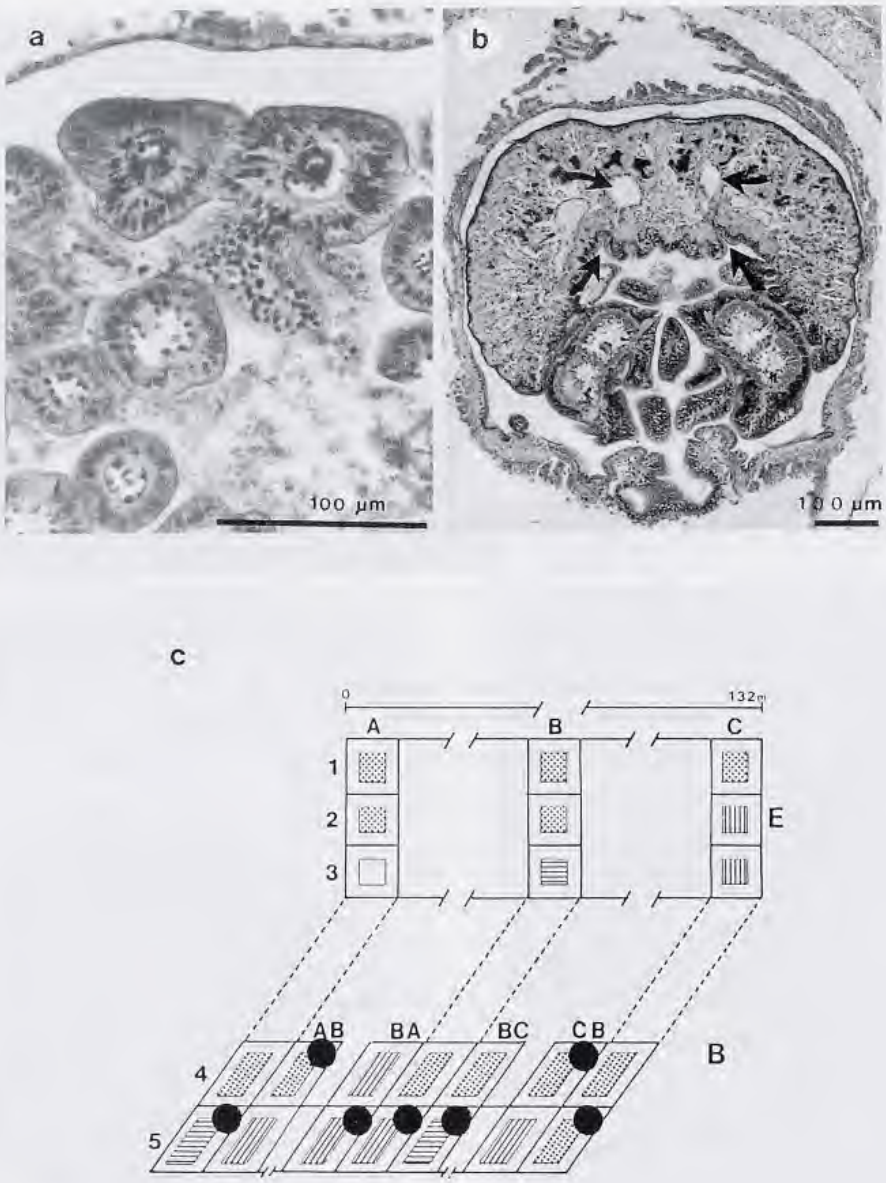



FIG. 4. — *Pherusa* sp.: **a**, beginning of the left ciliary groove on the branchial membrane. **b**, a section of the head showing the nephridia which also act as gonoducts (dorsal arrows) and the nephridiopores which also acts as gonopores (ventral arrows). **c**, study area 132 m wide; bank 5 m high (E); beach 36 m long (B); sampled beach 6 m long (comprised levels 4 and 5); transects A, AB, BA, B, BC, CB, and C; dotted pattern, low cohesion; vertical striped, medium cohesion; horizontal striped, high cohesion; plain, presence of *Pherusa sp.*

They are extensible, retractable, deciduous and rounded distally. The palp is horseshoe shaped with a ciliated almost straight base in the centre of which there is a ciliated slit (the ciliated groove of the palp) and a cavity separated by a septum. This separation of the cavity disappears towards the end of the palp. The circular and longitudinal muscles and the fluid-filled cavities of the palp form a hydrostatic skeleton. When the animal feeds, the ciliated base of the palps sweeps across the chaetal cage. The captured particles are moved by the cilia towards the medial groove. The ciliary current of the groove, which transports the particles, is rapid and arrives at the mouth passing between the dorsal and medial lips of each side.

Source : MNHN, Paris

The branchiae of *Pherusa* sp. arise from an achaetous segment between the first chaetiger and the head during the pelagic larval stage. They surround the prostomium in adults. They are filiform, contractile and ciliated along their length with an unusual distribution of cilia. There are between 80 and 90 branchiae divided into two groups on each side of the prostomium. The two groups are united dorsally by a pair of branchiae (Fig. 3a,b, and d). The dorsal branchiae are longest. The ciliated branchiae produce movement of the water and particles in suspension in the space limited by the chaetae of the first chaetiger. Food particles are concentrated and moved to the base of the two dorsal branchiae (Fig. 3d; Fig. 4a). The food particles are transported by the ciliary current of the prostomial grooves to the mouth. *Pherusa* sp. is a microphage and detritus feeder and feeds by day similar to other boring marine animals.

The two nephridiopores of *Pherusa* sp. are located in the branchial membrane near the internal line of branchiae and on each side of the prostomial ciliated grooves (Fig. 4b). Waste products and gametes are discharged through these pores.

The first 36 segments of the body are longer and wider than the rest which resembles a tail. The anus is located on the terminal portion. The tail is reflexed to give the body a U-shaped appearance. The mouth is ventral to the anus.

The population inhabits a loess which is covered with a dense growth of coralline algae. By systematically sampling the intertidal population, the density at Santa Elena was estimated to be 14 ind./100 $cm^2$. The species shows indirect development during November to February. Some of the larval stages can be collected by washing the coralline algae during this time.

The histochemical studies of the secretion of the tegumentary glands indicated the presence of acid mucopolysaccharides (Alcian blue at pH 5).

## DISCUSSION AND CONCLUSION

The paper by SPIES (1975) on the functional anatomy of the flabelligerid head was used as a basis for interpretation of the head.

Studies on the ecology of endolithic species of flabelligerids are limited. BLEAKNEY *et al.* (1980) mentioned *Flabelligera affinis* living in vacant burrows of the pelecypod *Zirfaea crispata*. This species is not a true endolithic worm since it does not burrow; it is a typical worm of cryptopfauna crevices.

*Pherusa* sp. is similar to a typical tubiculous animal in which the mouth, branchiae and nephridiopores are found in the anterior end. The anus is located at the posterior end of the body but the reflexed tail located the anus near the open end of the tube. All apertures of the body are at approximately the same level and near the opening of the tube.

The slightly acidic pH of the seawater within the tube could account for the absence of other organisms or ectoparasites on the body or within the tube. The acid mucopolysaccharids detected in the secretions of the tegumentary glands support the idea that *Pherusa* sp. possesses a chemical mechanism for burrowing in addition to a physical one.

Population density was estimated from 14 samples in which a high density, 14 burrows in 100 $cm^2$ with live animals was found in only seven suggesting that the population in the study area is distributed in dense patches of worms.

The lining of the tube is thicker around the aperture which could aid in establishing the burrow in substrates of low cohesion, but this thickening was also present in high-cohesion substrates.

The aragonite lining of the tube of *Pherusa* sp. could contribute to the cementation of the rock and increase its hardness in the same way as the calcite deposits of the burrow walls of *Lithophaga patagonica*, *Petricola patagonica*, and *Saxicava solida* which also inhabit the same area.

## REFERENCES

AMOR, A., LOPEZ ARMENGOL, M.F., IÑIGUEZ RODRIGUEZ, A.M. & TRAVERSA, L.P., 1991. — Intertidal endolithic fauna and it's relationship to the mineralogical, physical and chemical characteristics of the substrate. *Mar. Biol.*, **111** : 271-280.

Source : MNHN, Paris

BLEAKNEY, J.S., ROBINSON, S.M. & WAUGH, J.C., 1980. — Endolithic fauna of vacated *Zirfaea crispata* L. burrows in Blomidon shale, minas basin, Nova Scottia. *Proc. N.S. Inst. Sci.*, Nova Scotia, **30** : 55-63.

KRUMBAIN, W.C. & GRAYBILL, F.A., 1965. — *An introduction to statistical models in geology*. Mc Graw Hill Book Co., New York, 475 pp.

MARTOJA, R. & MARTOJA-PIERSON, M., 1967. — *Initiation aux techniques de l'histologie animale*. Masson et Cie., Paris, 345 pp.

SPIES, R.B., 1975. — Structure and function of the head in flabelligerid polychaetes. *J. Morph.*, **47** : 187-208.

Source : MNHN, Paris

# Polychaete fauna associated with the coral *Cladocora caespitosa* (L.) in the eastern Mediterranean

*Christos ARVANITIDIS & Athanasios KOUKOURAS*

Department of Zoology
University of Thessaloniki
540 06 Thessaloniki, Greece

ABSTRACT

Analysis of the polychaete fauna in 14 colonies of *Cladocora caespitosa* at two localities of Chalkidiki Peninsula, N. Aegean Sea, revealed 87 species, 58 of which are recorded for the first time as associated with this scleractinian coral. Larger colonies (up to 7 kg) contained more species, more individuals and a greater biomass. In one location, depth 3-5 m, Serpulidae were dominant (*Vermiliopsis infundibulum, Hydroides pseudouncinata pseudouncinata, Vermiliopsis striaticeps, Spirobranchus polytrema* and *Serpula vermicularis*) but at 16-19 m these were rivaled in abundance by errant species, especially *Ceratonereis costae*.

RÉSUMÉ

**Faune de polychètes associée au scléractiniaire *Cladocora caespitosa* (L.) en Méditerranée orientale**

L'analyse de la faune annélidienne trouvée dans 14 colonies de *Cladocora caespitosa* provenant de deux stations de profondeur 3-5 m et 16-19 m sur la péninsule de Chalkidiki, mer Egée, Nord de la Grèce, a montré qu'une faune diversifiée de polychètes est associée. Des 87 espèces récoltées, 58 sont reconnues pour la première fois comme hôtes de ce scléractiniaire. Dans la station à 3-5 m, les Serpulidae étaient dominants (*Vermiliopsis infundibulum, Hydroides pseudouncinata pseudouncinata, Vermiliopsis striaticeps, Spirobranchus polytrema* et *Serpula vermicularis*), alors qu'à 16-19 m ils étaient surpassés en abondance par des espèces errantes, en particulier *Ceratonereis costae*.

## INTRODUCTION

The coral *Cladocora caespitosa* (L., 1767), is unique among the scleractinian species living in the Mediterranean due to the presence of large zooxanthellate colonies. The diameter of its colonies may exceed 1m (ZIBROWIUS, 1980). The base and dead parts as well as the living parts of *C. caespitosa* provide suitable sites for attachment of many animal species. They may attach themselves to the surface, bore into the skeleton, or may be sheltered or confined within the interlacing branches. As a result, the associated fauna is highly diversified (VAUGHAN & WELLS, 1943; VAFIDIS, 1993).

ARVANITIDIS, C. & A. KOUKOURAS, 1994. — Polychaete fauna associated with the coral *Cladocora caespitosa* (L.) in the eastern Mediterranean. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 347-353. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

In the North Aegean Sea, *C. caespitosa* colonies may contribute significantly to the formation of submarine banks, together with other organisms, such as calcareous algae, sponges, polychaetes, etc. (KOUKOURAS & KÜHLMANN, 1991; KÜHLMANN *et al.*, 1991). Although it is well known that the fauna and flora in these banks are especially rich, information concerning the organisms associated is limited (LABOREL, 1961; LUMARE, 1967; SPADA, 1968; ZIBROWIUS, 1980 and VAFIDIS, 1993). Some data has been given by ZIBROWIUS (1968, 1969, 1979) and SCISCIOLI & NUZACCI (1970), concerning polychaetes living within these colonies. The present study provides additional information on the composition and the relationships of the macrobenthic communities associated with *C. caespitosa* colonies.

## MATERIALS AND METHODS

Sampling was carried out in autumn 1987 at two stations on Chalkidiki Peninsula (Fig. 1). At station 1 (Pirgadikia) the depth was 3 to 5 m and at station 2 (Vourvourou) it was 15 to 19 m. The colonies were detached from the substrate according to the method of McCLOSKEY (1970) and KOUKOURAS *et al.* (1985).

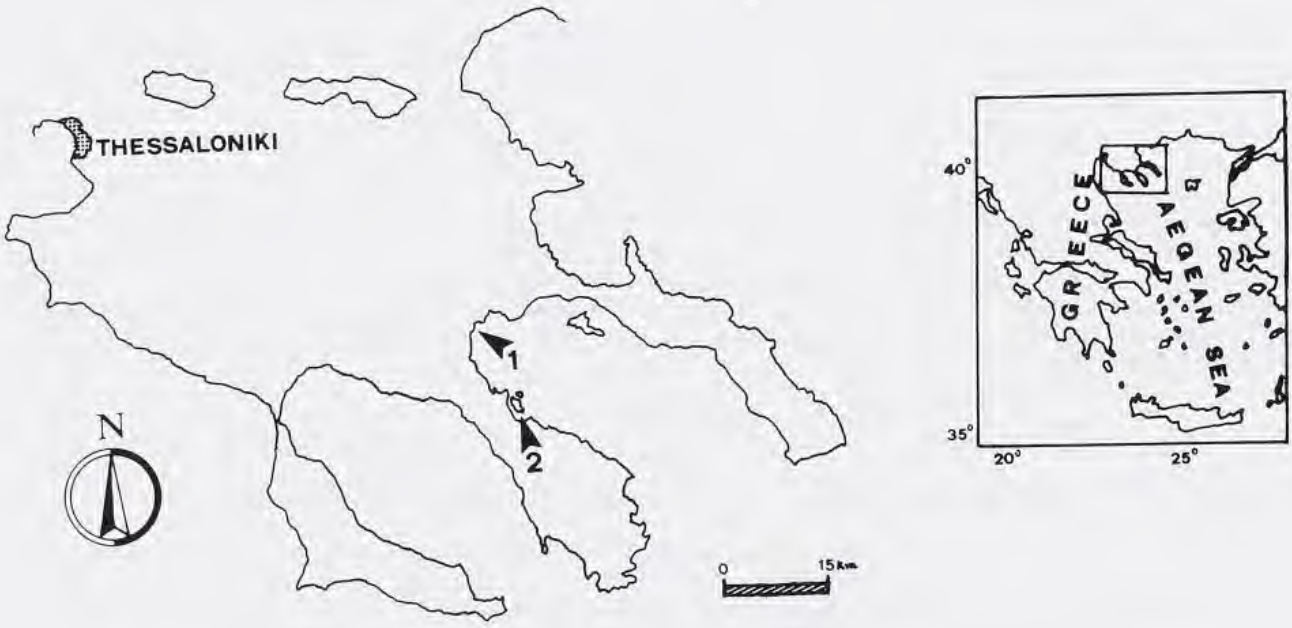



FIG. 1. — Map indicating the two sampling areas: 1, Pirgadikia (depth 3-5 m); 2, Vourvourou (depth 15-19 m).

Each colony was weighed and its volume measured by means of water displacement. The polychaetes present were identified to species and their dry biomass measured. The correlation between the volume and weight of colonies, on one hand, and the number of species, number of individuals and biomass of polychaetes, on the other, was based on the "rank correlation coefficient" or Spearman test (SCHWARTZ, 1963) since none of the above parameters was normally distributed. To estimate the faunal affinity between colonies, based on the polychaete composition, the quantitative coefficient given by CZEKANOWSKI (BRAY & CURTIS, 1957) was used, and the relevant dendrogram constructed as described by LANCE & WILLIAMS (DAGET, 1976). In order to quantify the contribution of the various species, the biological index, the frequency of appearance, the mean and cumulative dominance were estimated according to the methods proposed by GUILLE (1970).

Source : MNHN, Paris

## RESULTS

Table 1 lists the 87 polychaete species present in the 14 colonies examined. In figure 2, the positive correlation between the volume and weight of the colonies, on the one hand, and the number of species, individuals and biomass of the polychaetes on the other hand, can be seen.

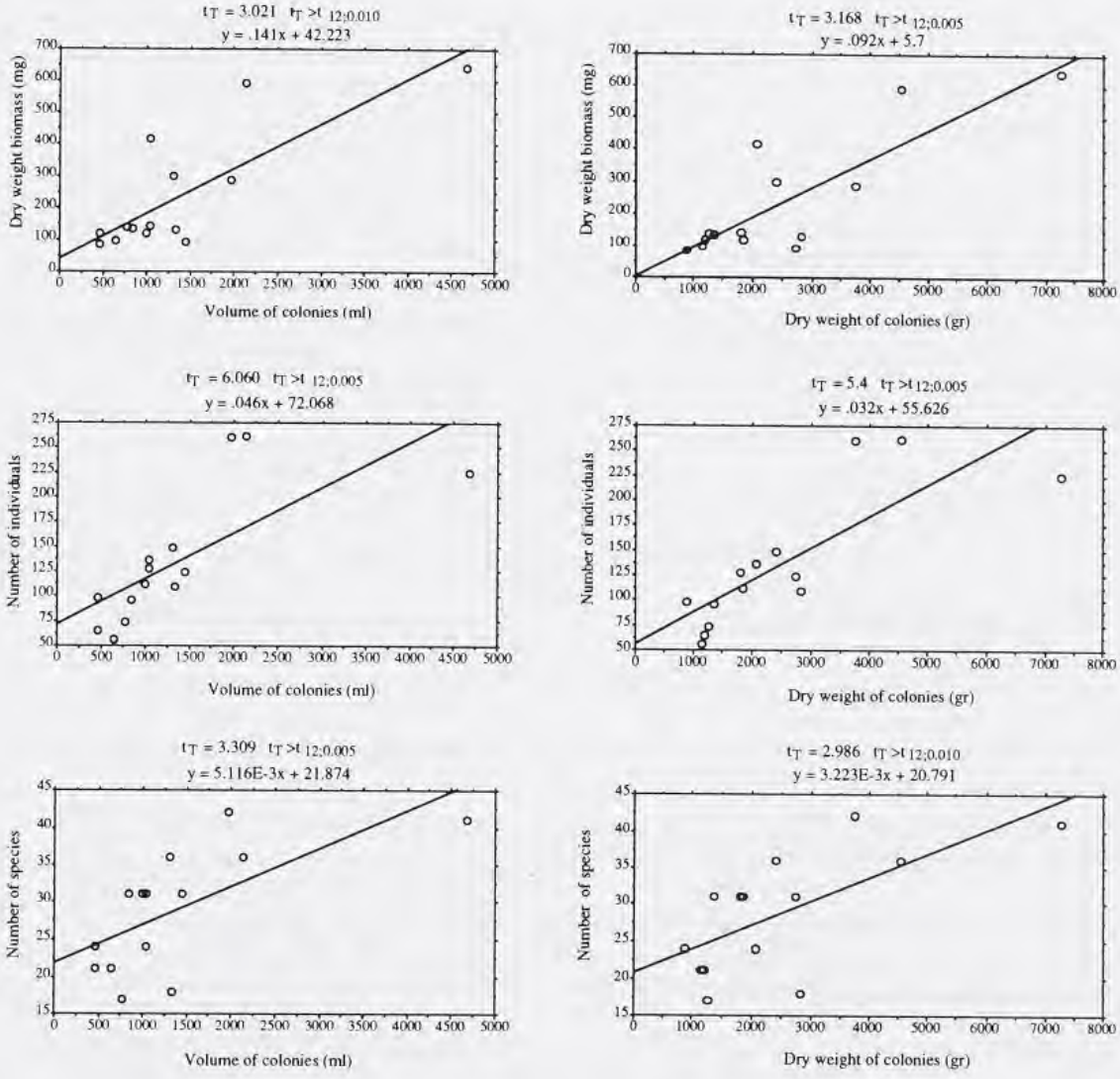



FIG. 2. — Correlations between volume and weight of the examined colonies and the number of species, individuals and dry weight biomass of polychaetes. Note: $t_{12;\,0.010} = 2.681$, $t_{12;\,0.005} = 3.055$.

A dendrogram groups the colonies according to the polychaete faunal affinity (Fig. 3). Symbols $C_1$-$C_7$ represent the colonies from the shallow station 1, $C_8$-$C_{14}$ the colonies from the deeper station 2 (Fig. 1). The colonies are divided into two groups corresponding to the two sampling stations with the exception of $C_{10}$. The highest affinity between colonies $C_{10}$ and $C_4$ could be attributed to these two colonies were among the most voluminous and heaviest and were the richest in number of individuals (262 in $C_4$ and 260 in $C_{10}$).

The 10 most abundant species are presented in Table 2 according to their biological indices a) for the total of the colonies (values marked with t), b) for the colonies coming from the shallow station 1 (values marked with s), and c) for the colonies coming from the deeper station 2 (values marked with d).

Source : MNHN, Paris

TABLE 1. — List of polychaete species found associated with *C. caespitosa* colonies. The species marked with a star are reported for the first time as inhabitants of this coral.

**Acrocirrus frontifilis* (Grube, 1860)
**Amphiglena mediterranea* (Leydig, 1851)
**Amphitrite variabilis* (Risso, 1826)
**Arabella iricolor* (Montagu, 1804)
**Bhawania reyssi* Katzmann, Laubier & Ramos, 1974
**Branchiomma bombyx* (Dalyell, 1853)
*Branchiomma* sp.
*Ceratonereis costae* (Grube, 1840)
**Cirriformia tentaculata* (Montagu, 1808)
**Dasybranchus gajolae* Eising, 1887
**Demonax brachychona* (Claparède, 1870)
**Dodecaceria concharum* Oersted, 1843
**Dorvillea rubrovittata* (Grube, 1855)
**Euclymene oerstedi* (Claparède, 1863)
*Eulalia viridis* (Linnaeus, 1767)
**Eumida sanguinea* (Oersted, 1843)
*Eunice* sp.
*Eunice torquata* Quatrefages, 1865
*Eunice vittata* (delle Chiaje, 1828)
*Euphrosine foliosa* Audouin & Milne Edwards, 1833
**Eupolymnia nebulosa* (Montagu, 1818)
**Eupolymnia nesidensis* (delle Chiaje, 1828)
*Eusyllis* sp.
**Glycera tesselata* Grube, 1863
**Goniada maculata* Oersted, 1843
**Haplosyllis spongicola* (Grube, 1855)
**Harmothoe antilopis* McIntosh, 1876
**Harmothoe areolata* (Grube, 1860)
**Harmothoe spinifera* (Ehlers, 1864)
**Heteromastus filiformis* (Claparède, 1864)
*Hydroides pseudouncinata pseudouncinata* Zibrowius, 1968
**Kefersteinia cirrata* (Keferstein, 1862)
*Leocrates chinensis* Kinberg, 1866
*Lepidasthenia elegans* (Grube, 1840)
**Lepidonotus clava* (Montagu, 1808)
**Lumbrineris coccinea* (Renier, 1804)
**Lumbrineris fragilis* (O. F. Müller, 1776)
**Lumbrineris funchalensis* (Kinberg, 1865)
**Lumbrineris latreilli* Audouin & Milne Edwards, 1834
*Lysidice ninetta* Audouin & Milne Edwards, 1833
**Marphysa fallax* (Marion & Bobretzky, 1875)
**Nainereis laevigata* (Grube, 1855)
**Nematonereis unicornis* (Grube, 1840)
*Nephtys* sp.
*Nereis rava* Ehlers, 1868
**Nereis zonata* Malmgren, 1867
*Nerinides* sp.
**Nicolea venustula* (Montagu, 1818)
**Notomastus latericeus* Sars, 1851
**Notophyllum* sp.
*Palolo siciliensis* (Grube, 1840)
**Perinereis cultrifera* (Grube, 1840)
**Petaloproctus terricola* Quatrefages, 1865
*Pherusa* sp.
*Phyllodoce* sp.
**Piromis eruca* (Claparède, 1870)
**Placostegus crystallinus* sensu Zibrowius, 1968
*Polycirrus aurantiacus* Grube, 1860
**Pomatoceros triqueter* (Linnaeus, 1767)
*Pontogenia chrysocoma* (Baird, 1865)
*Prionospio* sp.
**Proceraea* sp.
*Protula* sp.
**Pseudopotamilla reniformis* (O. F. Müller, 1788)
**Pterocirrus macroceros* (Grube, 1860)
*Sabella spallanzanii* (Viviani, 1805)
*Sabellaria spinulosa* Leuckart, 1849
**Schistomeringos rudolphi* (delle Chiaje, 1828)
**Sclerocheilus minutus* Grube, 1863
*Serpula concharum* Langerhans, 1880
*Serpula vermicularis* Linnaeus, 1767
**Sphaerosyllis pirifera* Claparède, 1868
**Sphaerosyllis* sp.
*Spirobranchus polytrema* (Philippi, 1844)
**Syllidia armata* Quatrefages, 1865
**Syllis gracilis* Grube, 1840
**Terebella lapidaria* Linnaeus, 1761
**Thelepus setosus* (Quatrefages, 1865)
**Trichobranchus glacialis* Malmgren, 1865
**Trypanosyllis zebra* (Grube, 1860)
**Typosyllis hyalina* (Grube, 1863)
**Typosyllis krohni* (Ehlers, 1864)
**Typosyllis prolifera* (Krohn, 1852)
**Typosyllis variegata* (Grube, 1860)
*Vermiliopsis infundibulum* (Gmelin, 1788)
**Vermiliopsis labiata* (Costa, 1861)
*Vermiliopsis striaticeps* (Grube, 1862)

Source : MNHN, Paris

Among the 10 abundant species (Table 2), six are sedentary forms, including five Serpulidae. The 10 abundant species comprise 63 % of the cumulative dominance (Table 2). The serpulid *Hydroides pseudouncinata pseudouncinata* Zibrowius, 1968 had the highest biological index and mean dominance. The serpulids *Vermiliopsis infundibulum* (L., 1788) and *Vermiliopsis striaticeps* (Grube, 1862) were next with significant difference in values of biological index and mean dominance. These three species showed a high value of cumulative dominance (28.24 %).

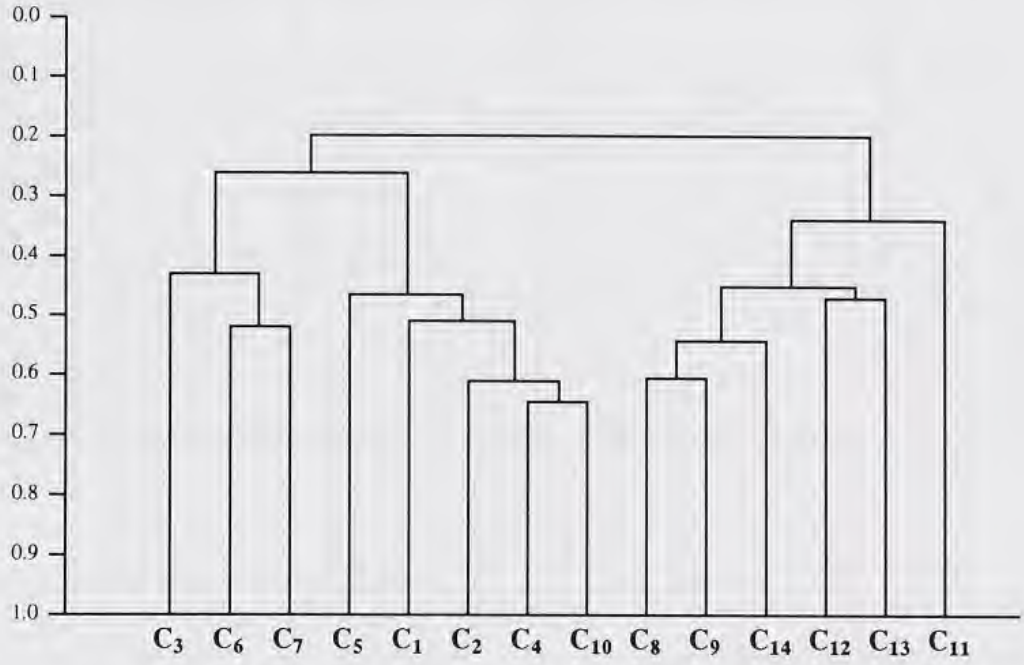



FIG. 3. — Dendrogram showing the polychaete faunal affinity among the *C. caespitosa* colonies.

In the colonies from the shallow station 1 (Table 2), the same species appeared in the first 10 of the biological index classification, except that *Lepidonotus clava* (Montagu, 1808) replaced *Ceratonereis costae* (Grube, 1840). Both these species are euryoecius and non-sedentary.

However, in the colonies from the deeper station 2 (Table 2), more significant differences existed both in relation to the shallow station 1 and to the total number of colonies examined. In the deeper water colonies, only four out of 10 dominant species were sedentary forms (three serpulids). Furthermore, in the colonies from the deeper station 2, the euryoecius non-sedentary species *Ceratonereis costae* (Grube, 1840) and *Kefersteinia cirrata* (Keferstein, 1862) are first and third in order of biological index; in the total of the colonies and in the colonies of the shallow water area, these two species are not at all classified or have a low biological index.

## DISCUSSION

Of the 87 polychaete species associated with the *C. caespitosa* colonies 58 are here reported for the first time as inhabitants of this coral where previously only 40 associated had been reported. The total number has been raised to 98, considering the species added by the present study.

The fact that serpulids were dominant in the colonies from the shallow station 1, whereas errant polychaetes were dominant in those from the deeper station 2, could be attributed to the different feeding opportunities offered by the different environment. Serpulids are filter feeders (FAUCHALD & JUMARS, 1979) and would benefit from water movement and from being near the source of primary production, whereas errant polychaetes being further up the food pyramid would mostly benefit from the sedimentation of material raining down from above and from other organisms living in the colonies.

Source : MNHN, Paris

TABLE 2. — Table of biological indices (Ib), frequency of appearance (F), mean dominance (Dm) and cumulative dominance (Dc) of polychaetes: a) in the total of the colonies (values marked with t), b) in the colonies from the shallow station 1 (values marked with s), c) in the colonies from the deeper station 2 (values marked with d).

| Species | Site (t) | Ib (t) | F (t) | Dm (t) | Dc (t) | Site (s) | Ib (s) | F (s) | Dm (s) | Dc (s) | Site (d) | Ib (d) | F (d) | Dm (d) | Dc (d) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Hydroides pseudouncinata* | 1 | 102 | 92.8 | 12.43 | 12.43 | 2 | 51 | 100 | 10.73 | 22.63 | 2 | 51 | 85.7 | 14.12 | 23.49 |
| *Vermiliopsis infundibulum* | 2 | 92 | 100 | 7.98 | 20.41 | 1 | 56 | 100 | 11.9 | 11.9 | 4 | 36 | 100 | 4.1 | 32.22 |
| *Vermiliopsis striaticeps* | 3 | 76 | 100 | 7.83 | 28.24 | 3 | 40 | 100 | 6.69 | 29.32 | 5 | 36 | 100 | 8.95 | 41.17 |
| *Kefersteinia cirrata* | 4 | 72 | 100 | 4.17 | 32.41 | 7 | 33 | 100 | 3.71 | 55.01 | 3 | 39 | 100 | 4.63 | 28.12 |
| *Spirobranchus polytrema* | 5 | 64 | 78.5 | 5.82 | 38.23 | 4 | 40 | 100 | 4.99 | 34.31 | | | | | |
| *Ceratonereis costae* | 6 | 60 | 71.4 | 5.13 | 43.36 | | | | | | 1 | 52 | 100 | 9.37 | 9.37 |
| *Serpula vermicularis* | 7 | 57 | 78.5 | 5.71 | 49.07 | 5 | 39 | 71.4 | 9.45 | 43.76 | | | | | |
| *Harmothoe spinifera* | 8 | 55 | 92.8 | 2.59 | 51.66 | 8 | 25 | 85.7 | 2.55 | 57.56 | 7 | 30 | 100 | 2.63 | 49.59 |
| *Pseudopotamilla reniformis* | 9 | 50 | 64.2 | 6.82 | 58.48 | 9 | 24 | 71.4 | 7.12 | 64.68 | 10 | 26 | 57.1 | 6.53 | 61.91 |
| *Notomastus latericeus* | 10 | 48 | 57.1 | 4.49 | 62.97 | 6 | 37 | 85.7 | 7.54 | 51.3 | | | | | |
| *Lepidonotus clava* | | | | | | 10 | 24 | 85.7 | 2.12 | 66.8 | | | | | |
| *Typosyllis hyalina* | | | | | | | | | | | 6 | 32 | 85.7 | 5.79 | 46.96 |
| *Haplosyllis spongicola* | | | | | | | | | | | 8 | 30 | 100 | 2.84 | 52.43 |
| *Polycirrus aurantiacus* | | | | | | | | | | | 9 | 30 | 85.7 | 2.95 | 55.38 |

## REFERENCES


BRAY, J.R. & CURTIS, J.T., 1957. — An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.*, **27** : 325-349.

DAGET, J., 1976. — *Les modèles mathématiques en écologie*. Ed. Masson, 172 pp.

GUILLE, A., 1970. — Bionomie benthique du plateau continental de la côte catalane francaise. II. Les communautés de la macrofaune. *Vie Milieu*, **21** : 149-280.

FAUCHALD, K. & JUMARS, P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. ann. Rev.*, **17** : 193-284.

KOUKOURAS, A., VOULTSIADOU-KOUKOURA, E., CHINTIROGLOU, H. & DOUNAS, C., 1985. — Benthic bionomy of the North Aegean Sea. III. — A comparison of the macrobenthic animal assemblages associated with seven sponge species. *Cah. Biol. mar.*, **26** : 301-319.

KOUKOURAS, A. & D.H.H. KÜHLMANN, 1991. — Rasenkorallen als Biotope in der Ägäis. *Naturw. Rundsch.*, **44** : 444-445.

KÜHLMANN, D.H.H., CHINTIROGLOU, H., KOUTSOUBAS, D. & KOUKOURAS, A., 1991. — Korallenriffe im Mittelmeer ? *Naturw. Rundsch.*, **44** : 316.

LABOREL, J., 1961. — Sur un cas particulier de concrétionnement animal. Concrétionnement à *Cladocora caespitosa* (L) dans le golfe de Talante. *Rapp. Comm. int. Mer Méditerr.*, **16** : 429-432.

LUMARE, F., 1967. — Sulla scogliera a *Cladocora* di Crotone e le sue biocenosi. *Rend. Accad. Naz.*, **16-17** : 101-131, pl. 1-3.

MCCLOSKEY, L.R., 1970. — The dynamics of the community associated with a marine scleractinian coral. *Int. Revue ges. Hydrobiol.*, **55** : 13-81.

SCISCIOLI, M. & NUZZACI, G., 1970. — Annelidi policheti associati a *Cladocora caespitosa* (L.) del litorale pugliese. *Att. Soc. Peloritana*, **16** : 151-157.

SPADA, G., 1968. — Osservazioni sull' habitat della *Coralliophila (Babelomurex) babelis* Réquien, 1848. *Conchiglie*, Milano, **4** : 170-176.

SCHWARTZ, D., 1963. — *Méthodes statistiques à l'usage des médecins et de biologistes*. Editions médicales Flammarion, Paris, 296 pp.


Source : MNHN, Paris

VAFIDIS, D., 1993. — *Systematical, zoogeographical and ecological study of Anthozoa (excluding Actiniaria) from the continental shelf of the North Aegean Sea*. Ph.D. Thesis, University of Thessaloniki, Thessaloniki.

VAUGHAN, T.W. & WELLS, J.W., 1943. — Revision of the suborders, families and genera of the Scleractinia. *Geol. Soc. America*, spec. Pap., **44** : 1-363.

ZIBROWIUS, H., 1968. — Étude morphologique, systématique et écologique des Serpulidae (Annelida Polychaeta) de la région de Marseille. *Rec. Trav. Stat. Mar. Endoume*, 59, Bull. **43** : 81-253.

ZIBROWIUS, H., 1969. — Quelques nouvelles récoltes de Serpulidae (Polychaeta Sedentaria) dans le golfe de Gabès et en Tripolitaine. *Bull. Inst. Océanogr. Pêche, Salammbô*, **1** : 123-137.

ZIBROWIUS, H., 1979. — Quelques récoltes de Serpulidae (Annelida Polychaeta) sur les côtes nord de la Tunisie. *Bull. Off. natn. Pêch. Tunisie*, **2** : 211-222.

ZIBROWIUS, H., 1980. — Les scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mém. Inst. océanogr.*, Monaco, **11** : 1-284.

Source : MNHN, Paris

Source : MNHN, Paris

# Morphology, ecology and juvenile development of *Cossura pygodactylata* Jones (Polychaeta, Cossuridae) in Arcachon Bay, SW France, with a reassessment of the geographical distribution of *C. pygodactylata* and *C. soyeri* Laubier

*Guy BACHELET* [*] *& Lucien LAUBIER* [**]

[*] Centre d'Océanographie et de Biologie marine
CNRS & Université de Bordeaux I
2, rue du Professeur Jolyet
33120 Arcachon, France

[**] Laboratoire de Physiologie des Etres Marins
Institut Océanographique
195, rue Saint-Jacques
75005 Paris, France

ABSTRACT

During a quantitative survey of subtidal infauna in Arcachon Bay (Bay of Biscay, NE Atlantic), more than 1,000 specimens of *Cossura* were collected in two muddy, shallow channels of the bay. Comparison of these specimens with the types of *C. pygodactylata* Jones, 1956 and *C. soyeri* Laubier, 1963 showed that the cossurids from Arcachon were almost identical with the former species. Only the noto- and neurosetal bundles of the first biramous setigers tended to be more spaced in the french specimens than in the holotype of *C. pygodactylata*; this minor divergence does not justify the erection of a new species. Examination of many juveniles, some of them being as small as four setigers, allowed the description of post-settlement juvenile development. During a two-year survey in the Courbey channel, the highest densities (ca. 1,500 ind./m$^2$) were recorded in April-May. As noted by several authors, there are few useful taxonomic characters in the genus *Cossura*. Specimens are often collected as anterior fragments, whereas species identification necessitates an examination of different regions of the body. For example, the two closely related species *C. pygodactylata* and *C. soyeri* differ only by the number of thoracic setigers and the structure of the pygidium. Re-examination of several specimens previously identified as *C. soyeri* showed that some of them were actually *C. pygodactylata*. The geographical distribution of *C. pygodactylata* is extended from the Pacific coast of North America to both sides of northern Atlantic, whereas *C. soyeri* appears to be restricted to the Mediterranean Sea and the northern Gulf of Mexico.

---

BACHELET, G. & L. LAUBIER, 1994. — Morphology, ecology and juvenile development of *Cossura pygodactylata* Jones (Polychaeta, Cossuridae) in Arcachon Bay, SW France, with a reassessment of the geographical distribution of *C. pygodactylata* and *C. soyeri* Laubier. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 355-369. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## RÉSUMÉ

**Morphologie, écologie et développement juvénile de *Cossura pygodactylata* Jones (Polychaeta, Cossuridae) dans le bassin d'Arcachon, SW France, et mise au point sur la distribution géographique de *C. pygodactylata* et *C. soyeri* Laubier**

Lors d'une étude quantitative de l'endofaune subtidale du bassin d'Arcachon (golfe de Gascogne, Atlantique NE), plus d'un millier de spécimens appartenant au genre *Cossura* ont été échantillonnés à faible profondeur (3 à 5 m) dans les fonds vaseux de deux chenaux. La comparaison de ces spécimens avec les types de *C. pygodactylata* Jones, 1956 et de *C. soyeri* Laubier, 1963 a montré que les cossuridés d'Arcachon sont identifiables à la première espèce. Seuls les faisceaux de soies des noto- et neuropodes des premiers sétigères biramés ont tendance à être davantage espacés chez les spécimens arcachonnais que sur l'holotype de *C. pygodactylata* ; cette divergence mineure ne justifie pas la création d'une nouvelle espèce. L'examen d'un grand nombre de juvéniles, à partir de stades à quatre sétigères, a permis la description des premières phases du développement benthique. Au cours d'un suivi de deux années dans le chenal du Courbey, les densités les plus élevées (environ 1500 ind./$m^{-2}$) ont été relevées en avril-mai. Ainsi que l'ont noté plusieurs auteurs, peu de critères taxonomiques sont utilisables dans le genre *Cossura*. Les spécimens sont souvent récoltés à l'état de fragments antérieurs, alors que l'identification spécifique nécessite l'examen des différentes parties de l'animal. Ainsi, les espèces voisines *C. pygodactylata* et *C. soyeri* diffèrent seulement par le nombre de sétigères thoraciques et la structure du pygidium. Un réexamen de plusieurs spécimens préalablement identifiés comme *C. soyeri* a montré que certains d'entre eux étaient en réalité des *C. pygodactylata*. La distribution géographique de *C. pygodactylata* est étendue de la côte Pacifique nord-américaine aux deux côtés de l'Atlantique Nord, alors que *C. soyeri* paraît limitée à la Méditerranée et au nord du golfe du Mexique.


## INTRODUCTION

Cossurids are small thread-like polychaetes characterized by a single median tentacle inserted on the dorsum of an anterior setiger. Other characters of the family Cossuridae Day, 1963 include a prostomium without appendages, reduced parapodial lobes, parapodia uniramous on one or more anterior segments or entirely biramous, all setae simple, and a pygidium with anal cirri (see EWING, 1987, for a revised diagnosis of the family). The family includes two genera, *Cossura* Webster & Benedict, 1887 with 17 species and *Cossurella* Hartman, 1976 with five species. The genus *Cossurella* is characterized as having a body distinctly divided into two regions and, in addition to simple setae, a single acicular seta in each ramus of the posterior parapodia (GARDINER & WILSON, 1977; EWING, 1987). Although FOURNIER & PETERSEN (1991) distinguished three body regions, there are no clear-cut divisions along the body in *Cossura* species, and all parapodia have only simple capillary setae.

As noted by DAY (1967), there are few useful taxonomic characters which may be used for identifying cossurids. The principal diagnostic features are the number of asetigerous peristomial segments, the segment of insertion of the mid-dorsal tentacle, the number of uniramous setigers, the types of setae, the number of thoracic setigers and the structure of the pygidium (EWING, 1984; FOURNIER & PETERSEN, 1991). Unfortunately, the number of peristomial segments appears to be an artifact of fixation, biramous setigers have been interpreted as uniramous by several authors when the bundles of setae were close together, and the posterior end is often missing (FOURNIER & PETERSEN, 1991; see below). The most important specific character in *Cossura* is the setiger from which the single dorsal appendage arises; although a greater or lesser part of the tentacle tip may be lost during collection and sieving, the entire structure is never broken off (THULIN, 1921; LAUBIER, 1963). FOURNIER & PETERSEN (1991) also found that the number of thoracic setigers might be, in spite of some local variation, species-specific. Taxonomic difficulties are not the unique problem in cossurids. Although occurring from shallow waters to abyssal depths, they are often recorded in low numbers and on a single occasion within a geographical area. Therefore, little is known about their ecology and population dynamics.

During a quantitative survey of macrobenthic assemblages in subtidal areas of Arcachon Bay, SW France, several specimens of *Cossura* sp. were collected in two muddy, shallow channels of the bay (DE MONTAUDOUIN, 1988). Later, while processing a collection of polychaetes collected during a two-year study of bivalve recruitment in one of the above channels (MADANI, 1989), one of us (GB) found more than 900 extra specimens of *Cossura*. These worms were tentatively identified as *C. soyeri* Laubier, 1963, which was the most commonly cited species in European temperate waters. However, comparison of our specimens with the types of *C. soyeri* Laubier and *C. pygodactylata* Jones, 1956 showed that the cossurids from Arcachon should be referred to the latter species. According to FOURNIER & PETERSEN (1991), both species belong to a group of *Cossura* with the dorsal branchial filament arising from the second setiger, but differ by the number of thoracic setigers (17-19 in *C. pygodactylata* vs. 30-31 in *C. soyeri*) and the shape of the pygidium.

Source : MNHN, Paris

In the present paper, we describe adult and juvenile stages of *C. pygodactylata* from Arcachon. To clear up the confusion between *C. pygodactylata* and *C. soyeri*, specimens from different collections are reexamined and the geographical distribution of both species is reassessed.

## MATERIAL AND METHODS

A total of 1,100 specimens of *C. pygodactylata* were obtained from mud in two channels, Courbey and Cousse, of Arcachon Bay (44°40'N, 1°10'W), at depths of 3-5 m below mean low water. In the Courbey channel, three stations were sampled monthly from February 1985 to January 1987, using a 225 $cm^2$ Ekman grab. Three replicate box-cores (depth of penetration generally 15 cm) were taken at each station, thus covering a total surface of 0.2 $m^2$ at each sampling date. Samples were fixed in 4 % buffered formaldehyde solution, then gently sieved through a 0.2 mm screen, transferred to 70 % alcohol and sorted after staining with Rose Bengal.

Samples were also collected in February 1988 in the Cousse channel and in a single station of Courbey channel. At both stations, six samples were taken using an Ekman grab. The content of four grabs was sieved on a 1.0 mm mesh; three 8 $cm^2$ cores were taken in each of the two other grabs and washed through sieves of 1.0 and 0.1 mm mesh opening. Samples were processed as above.

Specimens were studied using Wild stereomicroscope and compound microscope. Drawings were made by means of a camera-lucida drawing tube; measurements were made with an ocular reticule.

Specimens for SEM were transferred in glutaraldehyde, critical-point dried in carbon dioxide and individually mounted on aluminium stubs. After coating in gold, the specimens were viewed and photographed with a Jeol JSM-840A scanning electron microscope using an accelerating voltage of 10 kV.

### ***Cossura pygodactylata*** Jones, 1956

Figs 1-4

*Cossura pygodactylata* Jones, 1956: 127, fig. 1a-f. — REISH, 1958: 53, fig. 1. — LAUBIER, 1963: 840 (in key), 841 (in table). — HARTMAN, 1969: 273, figs 1-3. — FAUCHALD, 1972: 207 (in key). — ORENSANZ, 1976: 5 (in key). — FOURNIER & PETERSEN, 1991: 66, table 1.

*Cossura longocirrata* — BERKELEY & BERKELEY, 1956: 544, fig. 6. — ? BANSE, 1963: 204. — GIBBS, 1969: 314, table 1, 319, table 3, 324. — CURTIS, 1977: 31; 1979: 2. — ? RALLO, 1988: 137, 140, fig. 2 (*non* Webster & Benedict, 1887).

*Cossura*, nr. *longicirrata* — HARTMAN, 1954: 11, 15.

*Cossura candida* — HARTMAN, 1955: 44, *pro parte*.

*Cossura soyeri* — GARDINER & WILSON, 1977: 169, fig. 4a-c. — ? DAUVIN & GENTIL, 1980: 8. — BANSE, 1981: 633, *pro parte*. — HOBSON & BANSE, 1981: 55. — ? AGUIRREZABALAGA, 1984: 122 (in table). — ? AGUIRREZABALAGA *et al.*, 1984: 103. — ? SOLA & IBAÑEZ, 1986: 172, 173, 175 (in tables) (*non* Laubier, 1963).

*Cossura* sp. — DE MONTAUDOUIN, 1988: 18.

MATERIAL EXAMINED. — Eastern North Pacific: San Francisco Bay, off Point Richmond, California, mud, 16 Apr 1955, one complete specimen (Holotype, USNM 27609). — Orcas Island, Harney Pass, Washington, mud, Jul 1967, coll. H.L. Sanders, one complete specimen + 37 anterior ends (USNM 42014, labelled 25 specimens).

Western North Atlantic: Southport, North Carolina, black silt, 3-10 m, Sept 1976, coll. T. Finn, 10 ant. ends + one posterior end + three fragments of abdominal region (USNM 54141).

English Channel: Stonehouse Pool, Sta. 11, Plymouth Sound, silt/clay, 5 m, 25 Jul 1967, coll. P.E. Gibbs, four complete specimens + 16 ant. ends (BMNH ZB 1980. 341-360). — Bay of Morlaix, Brittany, France, muddy sand, 15 m, Apr 1980, four ant. ends, coll. J.C. Dauvin (Reference collection of Station Biologique de Roscoff).

Bay of Biscay: Courbey channel, Arcachon Bay, France, mud, 3-5 m, Mar 1985 - Feb 1988, 59 complete spec. + 723 ant. ends + five post. ends. — Cousse channel, Arcachon Bay, France, mud, 3 m, 15 Feb 1988, 109 complete spec. + 49 ant. ends + 27 post. ends [all specimens from Arcachon, coll. G. Bachelet; part of this material is deposited in the MNHN (UC 351)]. — Bidasoa estuary, Spain, sandy mud, 2.5 m, May 1992, coll. J.C. Sola, seven ant. ends (INSUB). — Basque coast, off San Sebastian, muddy sand, 100 m, Sta. G1, three ant. ends; Sta. G4, two ant. ends; Sta. G6, one ant. end; Sta. G8, five ant. ends. — Basque coast, off Bilbao, muddy sand, 100 m, Sta. B8, one ant. end (all specimens from Basque coast, coll. F. Aguirrezabalaga, INSUB). — Basque coast, off the Ría de Gernika, 100 m, coll. A. Rallo, 1 slide with one ant. end (UPV).

Source : MNHN, Paris

DIAGNOSIS. — A species of *Cossura* with dorsal tentacle arising from posterior margin of setiger 2. Proboscis with 4-8 finger-shaped processes. Setiger 1 uniramous, following setigers biramous. Thorax with 13-21 setigers. Pygidium with three long anal cirri (two dorsolateral and one mid-ventral) and 10-20 intercirral papillae. Juveniles without pygidial processes and with fewer thoracic setigers than adults.

## MATERIAL FROM ARCACHON

DESCRIPTION OF ADULTS (Figs 1-2). — Body is slender, threadlike, rounded in section, tapered to both ends. The longest complete specimen is 0.35 mm wide, 5.7 mm long for 43 setigers. The animals are usually colorless in alcohol, however some are uniformly yellow ochre.

The prostomium is bluntly conical, without appendages or eyespots, about twice as long as the peristomium. No nuchal organs have been observed. The peristomium is achaetous and without appendages, as long as the next segment. Some specimens seem to have two peristomial segments. However, when material is abundant within a sample, a complete gradation may be found, with some specimens apparently having two asetigers, others having a single asetiger, and others with only a slight, circular dip in the middle of the prostomium. In specimens with one peristomial segment, the mouth opens ventrally between the prostomium and peristomium. In those with two apparent asetigers, the buccal aperture is situated between these two "segments". Sagittal sectioning of anterior ends of such specimens does not show any septum in line with the prostomial dip. It is thus clear that there is only a single peristomial segment in our specimens, as found by JONES (1956) in *C. pygodactylata* from San Francisco Bay and by THULIN (1921) and FOURNIER & PETERSEN (1991) for *C. longocirrata*. The first apparent asetiger in some specimens is actually the basal portion of the prostomium which looks like a segment as longitudinal muscles contract (THULIN, 1921; JONES, 1956). The proboscis has been seen partially protruded in two worms only; according to JONES (1956), it terminates in 4-8 finger-shaped processes.

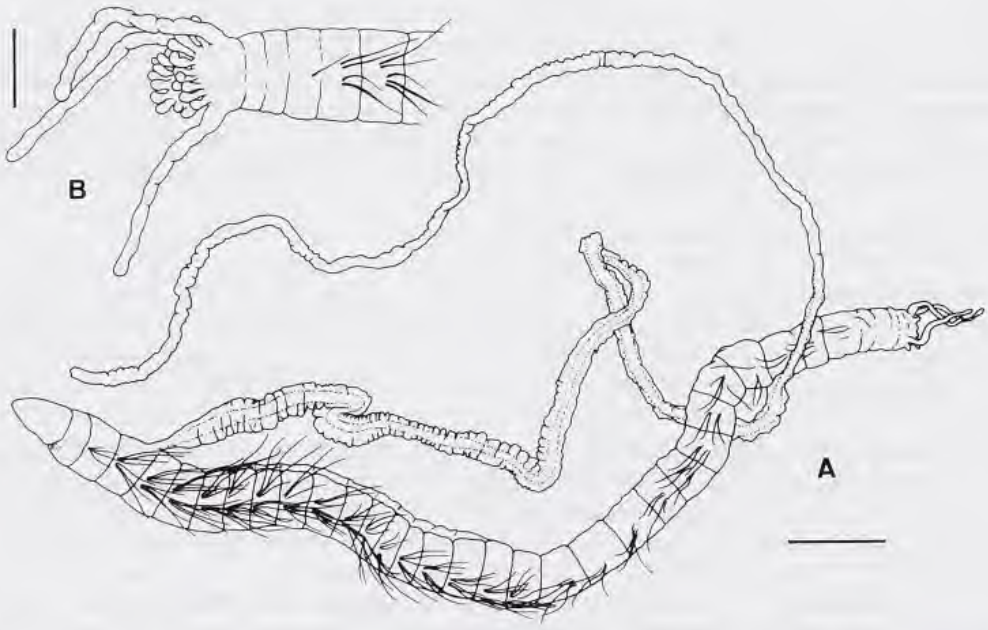



FIG. 1. — *Cossura pygodactylata* Jones, Arcachon Bay. A, entire worm, left lateral view. B, posterior end in lateral view. Scale bars : A = 200 µm, B = 75 µm.

The single median tentacle is inserted dorsally on the posterior end of the second setigerous segment. This branchial filament (BERKELEY & BERKELEY, 1956; LAUBIER, 1963; FOURNIER & PETERSEN, 1991) shows circular and irregular wrinkles over its whole length and is constricted near its point of insertion. The tentacle is usually longer than the body (up to 3x) but, due to its high contractility, there is no relationship between body length and tentacle length.

Source : MNHN, Paris

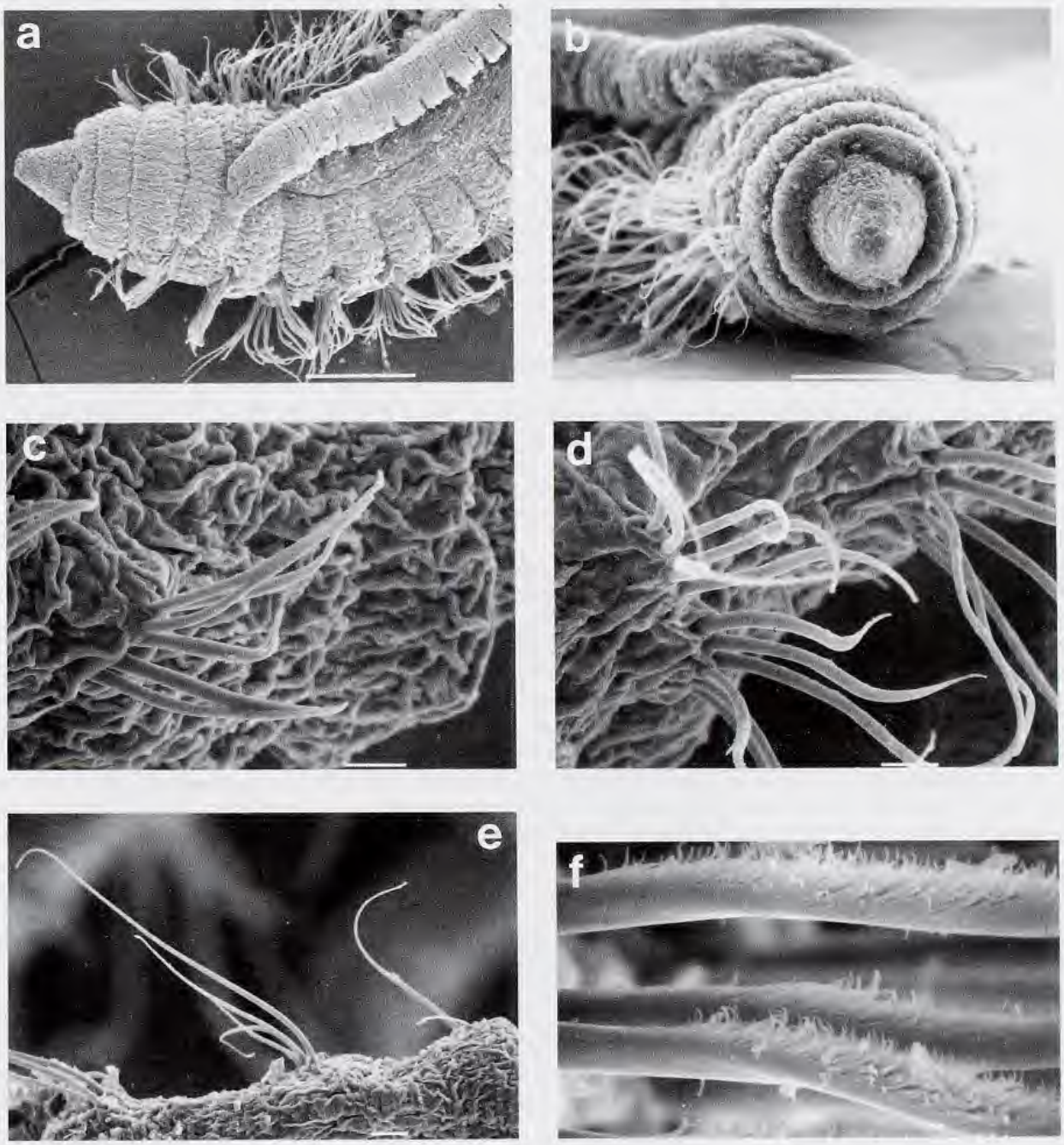



FIG. 2. — *Cossura pygodactylata*, SEM figures of adult specimens from Arcachon Bay. A, anterior end in dorsal view. B, same animal in frontal view. C, single bundle of setae of setiger 1, in posterior view. D, setiger 6 in dorso-lateral view. E, bundles of setae from posterior abdominal region, in lateral view. F, detail of capillary notosetae from setiger 2, in frontal view. Scale bars : A-B = 100 µm, C-E = 10 µm, F = 1 µm.

Source : MNHN, Paris

Although consisting of numerous similar segments, the body may be divided into three weakly separable regions according to the number and position of the setae in each segment and the respective length of setigerous segments. As in other cossurids there are no defined parapodial lobes and the setae arise directly from the lateral body wall.

The thoracic region extends to setiger 16-21; it is characterized by short (50-85 µm long), crowded segments with setae arising in bundles close to the anterior edge of each setiger. Setiger 1 is uniramous; thereafter all setigers are distinctly biramous. A mid-dorsal groove extends from the base of the unpaired tentacle over the whole thoracic region. As noted by LAUBIER (1963) in *C. soyeri* and FOURNIER & PETERSEN (1991) in *C. longocirrata*, some specimens have a transition zone of 1-2 setigers between the thorax and abdomen, where segmental length increases and setae migrate backwards; other specimens show more abrupt transition from anterior to mid-region.

In the abdominal region (7-20 setigers) segments are longer (70-160 µm) than in the thorax. Fragmentation always occurs within a few segments posterior to the thorax-abdomen transition, i.e. after setiger 17-30; this pattern seems to be characteristic (JONES, 1956; FOURNIER & PETERSEN, 1991). In some specimens there are poorly marked intersegmental constrictions in the mid-region; in others the abdomen takes on a moniliform aspect, with, for example, abdominal segments 160 µm long x 240 µm wide vs. thoracic segments 70 µm long x 170 µm wide measured on an entire specimen. The setae are similar to those of thoracic region and emerge from, or just behind, the middle of each segment. In ovigerous females, oocytes are present from setiger 19-20 to setiger 26.

The posterior region consists of 2-10 setigers followed by a few (2-3 ?), poorly marked achaetous segments. The segments are short and crowded, as in the thoracic region. The setae emerge mid-laterally of each segment and are smaller and fewer than in the abdomen.

The pygidium of adult specimens is cleft mid-dorsally and bears three long, thin anal cirri, 130-250 µm in length and 8-10 µm in diameter; one pair of cirri is inserted dorsolaterally on the edge of the anal lobes, whereas the third cirrus arises mid-ventrally. In addition to these cirri, 5-10 short (ca. 30 µm long) finger-like papillae are arranged laterally on the margin of each anal lobe. Cirri and papillae do not seem to be retractile.

The setae are all simple capillaries of two, slightly different kinds : shorter and thicker (4-5 µm wide) setae in the anterior row of thoracic setigers (see below), longer and thinner (2-3 µm wide) setae in the posterior row. Under transmitted light the setae appear to be slightly limbate and minutely spinulose along one margin; the ultrastructural arrangement of longitudinal filaments and the occurrence of very thin channels in the outer layer of the setae (SPECHT, 1988) also give the impression of longitudinally-striated shafts. SEM reveals that the setae are roughly cylindrical, have a smooth proximal shaft and are covered with dense, minute hairs along most of their length. This pilosity is directed upwards in neurosetae, downwards in notosetae.

The first setiger bears a single bundle of 5-7 setae on either side. The setae are arranged in two rows; the anterior row is composed of 2-4 short, fairly coarse, bluntly tapering setae which are directed perpendicular to the body; the posterior row consists of 2-4 longer, slender setae, tapering gradually towards the tips and slightly curved posteriorly. This setal arrangement in two parallel vertical series, i.e. an anterior row of setae thicker and shorter than those of a posterior row, persists in the biramous thoracic setigers; in these segments, there are 9-15 setae on either side, distributed in nearly equal numbers between the noto- and neuropodia (4-8 setae) and between the anterior and posterior rows. The highest number of setae (7-8 per ramus) is found in setigers 2-12. The setae of the anterior row project laterally, while those of the posterior row are directed posteriorly and dorsally in the notopodium, posteriorly and ventrally in the neuropodium.

In the abdominal region the setae are positioned mid-laterally in each segment, but without indication of rows. All setae become long, slender capillaries; their number decreases to 4-9 on either side. Progressively the tips of all setae tend to be directed forward. In the preanal region, the number of setae is gradually reduced to 1-4 on each side; all setae are thin capillaries, some are long (90-100 µm), whereas others (developing setae ?) are short (20-40 µm).

DESCRIPTION OF BENTHIC JUVENILES (Fig. 3). — Several morphological characters are common to both adults and juveniles: the shape of prostomium and peristomium, the mid-dorsal tentacle inserted on posterior margin of setiger 2, the lack of parapodial lobes, the first setiger uniramous, and the following setigers biramous. The most conspicuous differences between juveniles and adults lie in the body regions and the anal segment.

Segmentation is barely visible in young specimens. Therefore, the segmental length and the position of setal bundles on each segment cannot be used to distinguish body regions. However, with the exception of the very

Source : MNHN, Paris

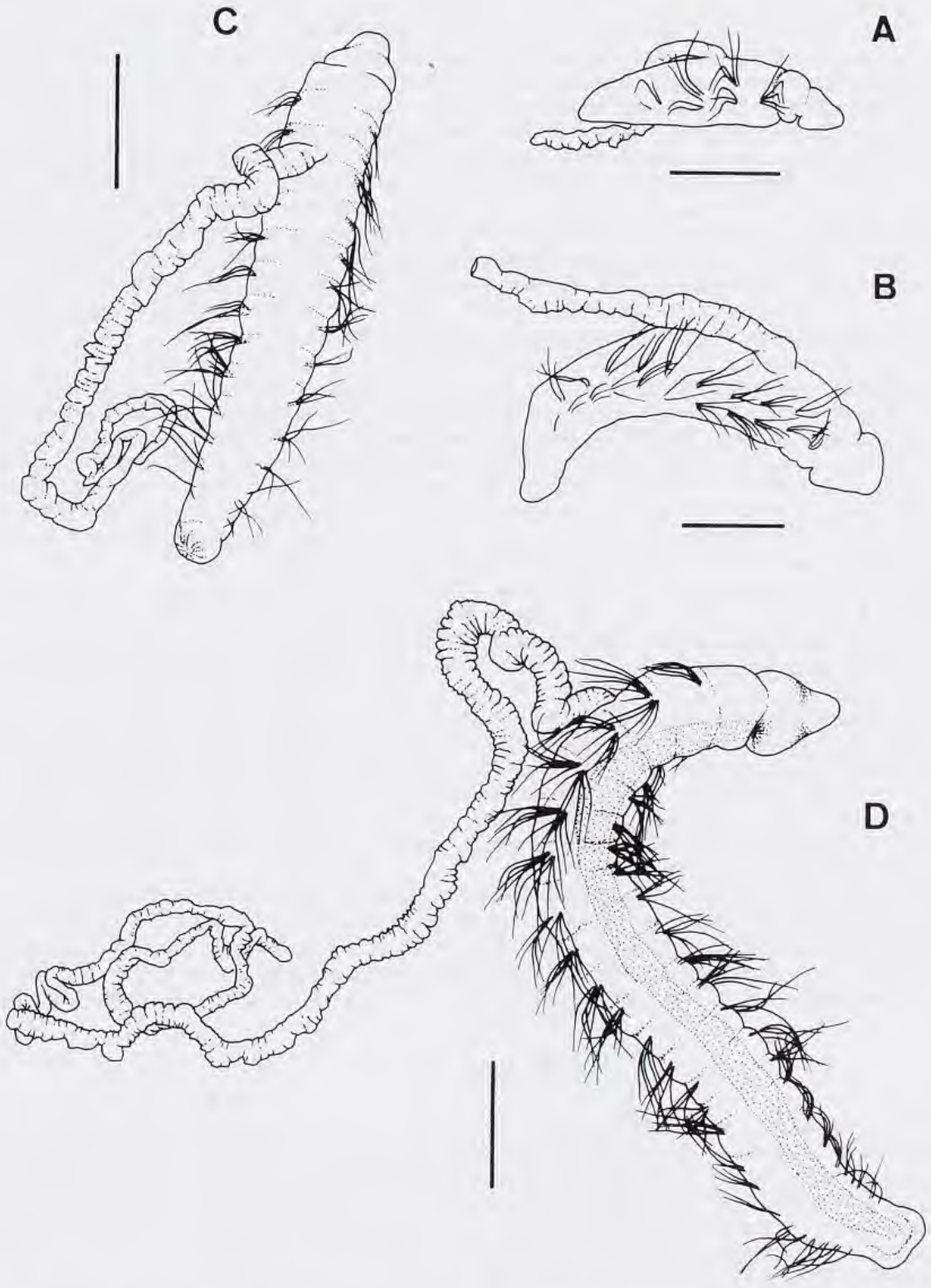



FIG. 3. — *Cossura pygodactylata*, benthic juveniles from Arcachon Bay. A, 4-setiger stage, lateral view. B, 11-setiger stage, lateral view. C, 14-setiger stage, dorsal view. D, 24-setiger stage, ventral view. Scale bars : A-B = 100 µm, C-D = 200 µm.

Source : MNHN, Paris

small worms, thorax and abdomen may be separated by observation of the setae. In the thoracic region, setae are numerous (4-5 on either side of setiger 1, 4-11 in each of the biramous setigers); they belong to the two types found in adults (i.e., some capillaries short and coarse, others long and thin) and are directed nearly perpendicular to the body axis. In the abdominal region, setae are fewer in number (2-6 per segment), all of the same slender type, and tilted forwards. The preanal region is poorly individualized, with one or two setigerous segments (with 1-2 short, fine capillaries) and a few segments devoid of setae.

The length of thoracic region changes during development. In the smallest specimen collected (four setigers, 245 µm long and 65 µm wide), the body cannot be divided into distinguishable regions. Ten-setiger stage worms, which are the next smallest specimens, are 400-500 µm long and have 7-8 thoracic setigers. The number of thoracic setigers gradually increases in longer worms until about 20 setigers are reached, which means that some abdominal segments of the early juveniles progressively change into thoracic segments. The total number of setigers also increases with the overall length, showing that growth occurs by addition of abdominal segments.

The pygidium of juveniles is devoid of terminal processes. FOURNIER & PETERSEN (1991) also noted that there were no anal cirri in very small specimens of *C. longocirrata*. In *C. pygodactylata* from Arcachon, the smallest specimens with both anal cirri and intercirral papillae were 26-setigers long.

ECOLOGY AND POPULATION DYNAMICS. — In the Bay of Arcachon, *C. pygodactylata* was collected in two shallow channels where bottom water temperature fluctuated between 7 °C (January) and 21 °C (August); annual salinity range was 27-34 P.S.U.. Highly developed seagrass (*Zostera marina*) beds induce an increased sedimentation of fine particles in both sites, which are also relatively sheltered from strong tidal currents and waves (BOUCHET, 1968). Sediment is an organic-rich (loss on ignition: 11.2 %) black mud (silt-clay content: 60.1 % in Courbey channel, 73.7 % in Cousse channel); only the top 2-3 mm layer is oxidized. As deep as the grab penetrates, mud is mixed with high quantities of decaying leaves of *Zostera* spp. (16.5 % in dry weight in Courbey channel, and 27.9 % in Cousse channel) (DE MONTAUDOUIN, 1988).

Horizontal sectioning of some cores showed that *C. pygodactylata* lives in the upper 2 cm layer of mud. As observed by THULIN (1921) and JONES (1956), cossurids produce loosely constructed tubes: in some worms, part of the body is faintly wrapped in membranous fragments, incrusted by very fine mineral grains. Diatoms and sand grains are often seen by transparency in the gut; cossurids were classified as subsurface deposit-feeders by FAUCHALD & JUMARS (1979).

Although most specimens collected at Arcachon were juvenile stages, some ovigerous females were found every year from February to April. The yolky oocytes were oval and about 110 µm long by 70 µm wide; these sizes are smaller than those given by JONES (1956) for *C. pygodactylata* (140 µm x 100 µm) and BANSE (1981) for *C. soyeri* (150 µm x 100 µm), but larger than those found by FOURNIER & PETERSEN (1991) in *C. longocirrata* (75 µm x 35 µm); however, these dimensions may refer to different developmental stages. In all our specimens, the number of oocytes never exceeded eight per segment, whereas, in the same species, JONES (1956) noted that a single segment might contain as many as 40.

Figure 4 shows the seasonal pattern of abundance in the Courbey channel with recruitment peaks of ca. 1,500 ind./m$^2$ in April 1985 and May 1986. Densities were considerably higher in February 1988 in the Courbey and Cousse channels, with 4,800 and 32,000 ind./m$^2$ respectively. Numbers dramatically decreased in the next one or two months following recruitment and the population almost disappeared until the next spring. A similar collapse of bivalve populations in the Courbey channel has been ascribed to summer oxygen deficiency by MADANI (1989).

## OTHER MATERIAL

In his description of *C. pygodactylata*, JONES (1956) indicated that "the 1st setiger bears a bundle of about six setae on either side"; then "the 2nd to 6th setigers carry approximately 12 setae on either side, and all setae, to the 6th setiger, appear to arise with no indication of noto- and neurosetal bundles", and "at about the 7th to 8th setiger, it is possible to differentiate noto- and neurosetal bundles" (p. 128). These assertions have been differently interpreted by various authors. Following REISH (1958) who indicated in the legend of his figure 1 that "the setae of the notopodium and neuropodium [in setigers 1-6] are *continuous*", LAUBIER (1963), FAUCHALD (1972) and ORENSANZ (1976) gave keys of the family Cossuridae with *C. pygodactylata* having 6-7 *uniramous* anterior setigers; however, REISH used the same symbol (the single letter S in his figure 1) for the 1st setiger of *C. delta* in which "the first setigerous segment is *biramous* with the setae forming a *continuous* lateral series" (REISH, 1958: 54). On the other hand, HARTMAN (1969: 273) noted in her diagnosis of *C. pygodactylata*: "third segment the first

Source : MNHN, Paris

setigerous, its setae in *biramous* fascicles, as are those farther back". Therefore, it seems that there has been some confusion in the interpretation of JONES's description of *C. pygodactylata*, as was also the case with *C. longocirrata* (FOURNIER & PETERSEN, 1991). Reexamination of the holotype of *C. pygodactylata* definitely shows that setiger 1 is uniramous, with six setae on either side; in the next five setigers, the setae form almost a continuous series but, by transparency, it may be seen that the setae originate clearly from two muscular sheaths on either side (suggested by JONES's figure 1b); the last thoracic setigers are distinctly biramous. In most specimens from Arcachon the noto- and neurosetal bundles of the first biramous setigers (from setiger 2) are more spaced than in the holotype; in few of them, however, the rami of biramous setigers are also very close together. Other characters of the holotype, especially the number of thoracic setigers and the structure of the pygidium, are consistent with JONES's description.

All specimens herein re-identified as *C. pygodactylata* have in common a single uniramous setiger, the dorsal tentacle inserted on posterior margin of setiger 2 and 13-21 thoracic setigers (Table 1). Although diverging a little from the range found in type specimens (17-19), this difference in the number of thoracic setigers does not appear to be taxonomically significant.

Very few specimens are complete. When present, the pygidium has always three long anal cirri and a large number (10-19) of intercirral papillae. In the collection from Plymouth, these papillae are present in two specimens with 20 and 22 setigers, i.e. at a smaller size than at Arcachon. It is also notable that, over the hundreds of specimens examined, none exhibits a protruded proboscis; a single worm, collected by J.C. SOLA, San Sebastian, in the Bidasoa estuary, has a partially protruded buccal organ. In freshly collected specimens from the Bidasoa, the dorsal tentacle shows a central, red blood vessel throughout its length.

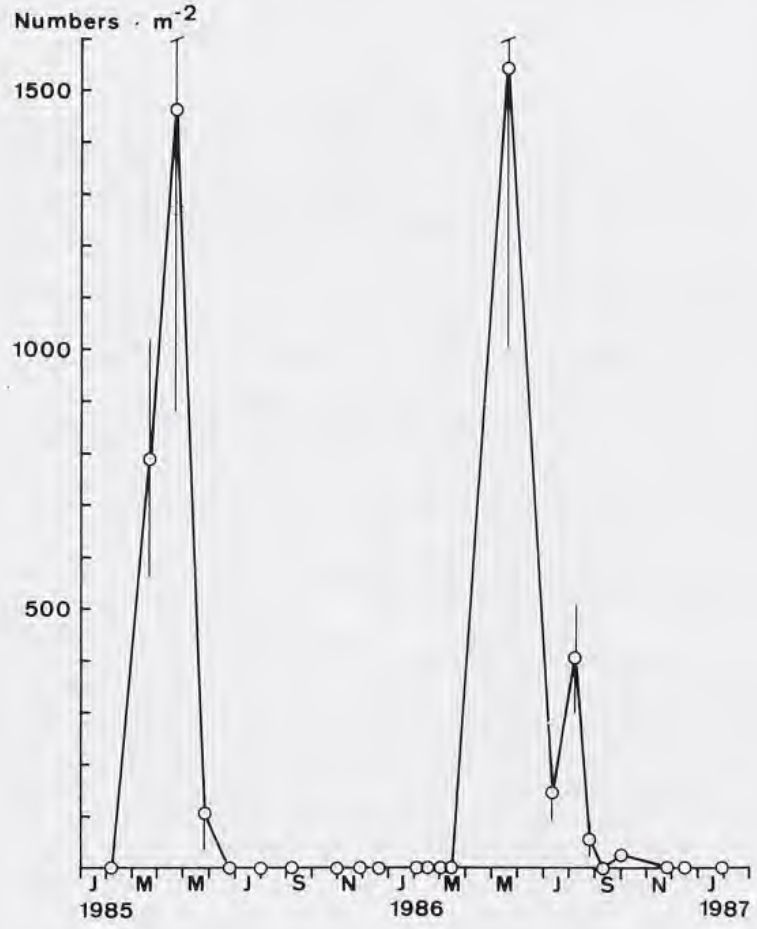



FIG. 4. — Seasonal mean abundance (±1 S.D.) of *Cossura pygodactylata* in the Courbey channel, Arcachon Bay, from February 1985 to January 1987.

Source : MNHN, Paris

The number and size of oocytes vary between locations. In an anterior fragment collected in September in North Carolina, there are about 30 oocytes (70 µm x 35 µm) per segment, i.e. a similar number of oocytes, but smaller by half in size, than those found in April in California (JONES, 1956). Other specimens have considerably fewer oocytes in each segment, as those from Arcachon: eight oocytes (100 µm x 80 µm) in the Bidasoa estuary (May), six oocytes (80 µm x 60 µm) in Plymouth Sound (July), or even four oocytes (80 µm x 40 µm) in the worm collected by RALLO (1988).

There remains some doubt about the identity of specimens from the Bay of Morlaix and the Spanish Atlantic coast where complete worms have never been collected (Table 1). The number of thoracic setigers recorded in these worms is characteristic both of *C. pygodactylata* and *C. longocirrata*; only the structure of the pygidium, with numerous intercirral processes in the former species and none in the latter, differs between both species (FOURNIER & PETERSEN, 1991). However, due to the arctic-boreal distribution of *C. longocirrata* (FOURNIER & PETERSEN, 1991) and the neighbouring occurrence of *C. pygodactylata* at Plymouth and Arcachon, the specimens of *Cossura* from Morlaix and the Basque coast are likely to be referable to *C. pygodactylata*.

REMARKS. — BANSE (1981) examined specimens from several sites in Washington, that he referred to as *C. soyeri*. It may be inferred from his description that the abdominal region begins after the first 30 setigers (p. 633). However, he reported further (p. 634) that some animals had segments from about setiger 17 packed with oocytes. Some of these specimens have been reexamined by us and identified as *C. pygodactylata*; in this lot (USNM 42014) there was also an anterior fragment of 19 setigers and 2.2 mm long, with the dorsal tentacle inserted on the posterior margin of setiger 3 (probably "*Cossura* sp." in BANSE's paper, p. 634). Specimens of *Cossura* from this area may belong to two or three species.

## ***Cossura soyeri*** Laubier, 1963

Fig. 5

*Cossura soyeri* Laubier, 1963: 833, fig. 1a-h; 1965: 137. — REYSS, 1971: 542, table 1, 552, 609, table 21. — FAUCHALD, 1972: 207 (in key). — ORENSANZ, 1976: 5 (in key). — ? BANSE, 1981: 633, *pro parte*. — ? HOBSON & BANSE, 1981: 55. — ? AMOUREUX, 1982: 184. — ? LOPEZ-JAMAR, 1982: 261, table 2. — EWING, 1984: 4-4, 4-6, fig. 4-4a-d. — ? SALAZAR VALLEJO & DONATH HERNANDEZ, 1984: 61, fig. 1a-c. — GAMBI & GIANGRANDE, 1986: 852, table 1. — ? LOPEZ-JAMAR & MEJUTO, 1986: 98, 101, 103 (in tables). — ? ROSENFELDT, 1989: 214, 234. — FOURNIER & PETERSEN, 1991: 66, table 1.

*Cossura soyerii* - DESBRUYÈRES, GUILLE & RAMOS, 1972: 357 (in table).

*Cossura sojeri* - COGNETTI-VARRIALE & ZUNARELLI-VANDINI, 1978: 42, table 1.

*Cossura* cf. *soyeri* - ? AMOUREUX, 1987: 574.

*Cossura longocirrata* - ? BANSE, 1963: 204 (*non* Webster & Benedict, 1887).

Not *Cossura soyeri* - GARDINER & WILSON, 1977: 169, fig.4 a-c. — DAUVIN & GENTIL, 1980: 8. — AGUIRREZABALAGA, 1984: 122 (in table). — AGUIRREZABALAGA *et al.*, 1984: 103. — AGUIRREZABALAGA, IBANEZ & ROS, 1986: table 1. — SOLA & IBAÑEZ, 1986: 172, 173, 175 (in tables).

MATERIAL EXAMINED. — Western Mediterranean Sea: off baie du Troc, Banyuls-sur-Mer, France, mud, 35 m, 27 June 1962, one anterior end (Holotype, LA 1052 GIIIa); 16 Jun 1962, one ant. end (Paratype, LA 1051 GIIIa). — ? Banyuls-sur-Mer, France, one complete specimen + one ant. end (LA, with paratype). — off Palavas-les-Flots, Languedoc, France, muddy sand, 20-25 m, Jun 1991, 18 ant. ends, coll. J.M. Amouroux (LA).

Gulf of Mexico: off Florida, Sta. 12, 90 m, Nov 1980, three ant. ends (USNM 89499); Sta. 33, 145 m, Jul 1981, one ant. end (USNM 89500). — Off Mississippi, Sta. VI — 2638, 24 m, Jun 1975, three ant. ends (USNM 75148). - South Timbalier Lease area, off Louisiana, Sta. 03P, 30 m, Jan 1979, one ant. end (USNM 89504). — Off Port Aransas, Texas, Sta. II-1, 22 m, Nov 1976, three ant. ends (USNM 89501); Sta. II-4, 36 m, Nov 1976, two ant. ends (USNM 89503); Sta. II-1, Dec 1976, three ant. ends (USNM 89502).

Eastern North Pacific: Bahia de San Quintin, Sta. 4, Baja California, Mexico, 4 Dec 1981, numerous dried specimens, coll. L.E. Calderon Aguilera (CICESE).

DIAGNOSIS. — A species of *Cossura* with dorsal tentacle arising from posterior margin of setiger 2. Proboscis with about seven short processes. Setiger 1 uniramous, following setigers biramous. Thorax with 20-31 setigers. Pygidium with three long anal cirri (two dorsolateral and one mid-ventral), without intercirral processes.

Source : MNHN, Paris

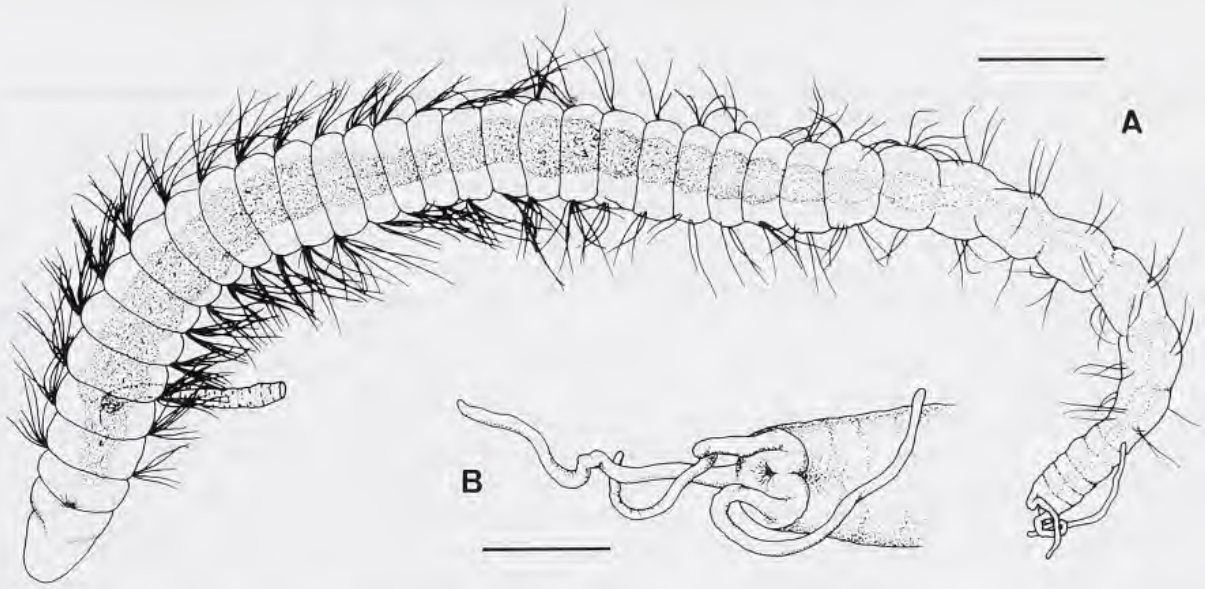



FIG. 5. — *Cossura soyeri* Laubier, Banyuls-sur-Mer, "specimen B". A, entire worm in ventral view, dorsal tentacle broken. B, posterior end in ventral view. Scale bars : A = 200 mm, B = 100 mm.

REMARKS. — The holotype and paratype are anterior fragments, with 39 and 21 setigers respectively; in the original description two "peristomial segments" were counted, increasing the number of segments to 41 and 23, respectively. In the holotype the first 28 setigers are similar in shape, with setae arising in bundles at the anterior edge of each segment; setigers 29-31 become increasingly longer and the setal bundles migrate posteriorly; the last eight setigers are abdominal setigers, about twice as long as thoracic setigers, and with setae emerging from the middle of segments.

Within the vial containing the paratype, there was a tube with two specimens, hereafter designated A and B. Specimen A is an anterior end, about 2.1 mm long and 0.36 mm wide, with 23 setigers; this specimen is dark brown in color, as are the holotype and paratype, and is likely to be the third *C. soyeri* collected by LAUBIER (1963, 1965) off the baie du Troc. The 23 setigers of specimen A, as well as the 21 setigers of the paratype, are all thoracic setigers. Specimen B is a complete worm, 2.6 mm long, 0.17 mm wide, with 33 setigers; its origin is unknown but it might have been collected in the area of Banyuls-sur-Mer. The first 23 setigers are similar in shape (about 55 µm long), separated by marked intersegmental constrictions, as in most specimens reexamined. The abdominal region consists of 10 setigers, longer (100-110 µm) and with fewer setae than in the thorax. The preanal region consists of only five short (about 20 µm long), achaetous segments. The pygidium has a slight mid-dorsal cleft and bears three long anal cirri, one pair lateral and the other midventral; there are no intercirral processes. Although the first 23 setigers are "thoracic" by their shape, the number of setae decreases by setiger 19-20 and the setae become more posterior in each segment.

The longest specimen collected off Palavas is an anterior fragment of 0.35 mm wide and 6.7 mm long for 45 setigers; the anterior region extends to setiger 26, as in an other incomplete worm of 28 setigers. Setigers are all thoracic in the other 16 anterior ends (17-29 setigers). In this collection, most specimens show a partially protruded proboscis; in one of them, the proboscis is globular and terminates in seven short processes.

Several specimens from the Gulf of Mexico are damaged posteriorly; the transition from thorax to abdominal regions is difficult to determine in these specimens. Nevertheless, six anterior ends with 20-30 setigers have only thoracic segments. In two anterior ends of 21 setigers (USNM 89499) the thoracic region extends to setiger 20. In the longest anterior fragment (USNM 89501: 4.0 mm long, 33 setigers) the thoracic region consists of 29 setigers. In complete specimens from the same area, EWING (1984) observed and figured (fig. 4-4d) a pygidium with three filamentous caudal cirri, similar to the pygidium of specimen B.

The principal morphological characters of all reexamined specimens of *C. soyeri* are summarized in Table 1.

Source : MNHN, Paris

TABLE 1. — Comparison of the main morphological characteristics of specimens referred to as (1) *Cossura pygodactylata* Jones and (2) *C. soyeri* Laubier in the present paper. Data from reexamination of specimens unless otherwise specified.

| | Number of thoracic setigers | | | First setiger with oocytes | Structure of pygidium | Record reference |
|---|---|---|---|---|---|---|
| | Range | Average | n | | | |
| (1) ***Cossura pygodactylata*** Jones | | | | | | |
| San Francisco Bay, California | 17-19[a] | - | - | 18-20 ?[a] | 3 anal cirri + 12-20 papillae[a] | JONES (1956: *C. pygodactylata*) |
| Orcas Island, Wash. | 16-17[b] | - | - | - | 3 anal cirri + papillae[c] | BERKELEY & BERKELEY (1956: *C. longocirrata*) |
| " | 17-21 | 18.8 | 20 | - | 3 anal cirri + 12 papillae | BANSE (1981: *C. soyeri*) |
| Disco Bay, W Greenland | ? | - | - | - | 3 anal cirri + papillae[b] | CURTIS (1977, 1979: *C. longocirrata*) |
| Southport, N Carolina | 14-16 | 15.0 | 5 | 16 | 3 anal cirri + 12 papillae | GARDINER & WILSON (1977: *C. soyeri*) |
| Plymouth Sound, England | 14-18 | 16.1 | 20 | 18 | 3 anal cirri + 10-12 papillae | GIBBS (1969: *C. longocirrata*) |
| Bay of Morlaix, France | 14-17 | 16.0 | 3 | - | (missing) | DAUVIN & GENTIL (1980: *C. soyeri*) |
| Arcachon Bay, France | 16-21 | 17.5 | 37 | 19-20 | 3 anal cirri + 10-19 papillae | this study |
| Bidasoa estuary, Spain | 14-17 | 16.4 | 7 | 19 | (missing) | SOLA & IBAÑEZ (1986: *C. soyeri*) |
| Basque coast, Spain | 21[d] | - | 1 | - | (missing) | AGUIRREZABALAGA (1984: *C. soyeri*) |
| " | 13-20 | 16.7 | 10 | 21 | (missing) | AGUIRREZABALAGA, IBAÑEZ & ROS (1986: *C. soyeri*) |
| " | 18 | - | 1 | 19 | (missing) | RALLO (1988: *C. longocirrata*) |
| (2) ***Cossura soyeri*** Laubier | | | | | | |
| Banyuls-sur-Mer, French Mediterranean | 28 or 31 | - | 1 | 32? | (missing) | LAUBIER (1963: *C. soyeri*) |
| " | 23 | - | 1 | - | 3 anal cirri | this study |
| Languedoc, French Mediterranean | ≥ 26 | 26.0 | 2 | - | (missing) | this study |
| Gulf of Mexico | 20-≥30 | 23.0 | 3 | - | 3 anal cirri[e] | EWING (1984: *C. soyeri*) |

[a] JONES (1956). [b] FOURNIER & PETERSEN (1991). [c] Three lobes between each pair of cirri, according to BERKELEY & BERKELEY (1956), but at least five lobes and several stubby intercirral processes, according to FOURNIER & PETERSEN (1991). [d] A.H. ARIÑO, Pamplona (pers. comm.). [e] EWING (1984).

## GEOGRAPHICAL DISTRIBUTION

Records of *C. pygodactylata* have been infrequently listed in the literature, perhaps because of the non-occurrence of the characteristic pygidium in most collected specimens and also the possible confusion with both *C. longocirrata* (FOURNIER & PETERSEN, 1991) and *C. soyeri*. Originally recorded from central – San Francisco Bay (HARTMAN, 1954, 1955; JONES, 1956) – and southern California – Hueneme canyon, off Los Angeles (HARTMAN, 1969) –, *C. pygodactylata* is also present more northerly in the Eastern North Pacific, i.e. in British

Source : MNHN, Paris

Columbia (FOURNIER & PETERSEN, 1991). The present study extends its geographic distribution to the Western (North Carolina) and Eastern North Atlantic (English Channel, Bay of Biscay). The species may also be present in Disko Bay, West Greenland, where specimens referred to *C. longocirrata* by CURTIS (1977, 1979) have been reexamined and identified as *C.* cf. *pygodactylata* by FOURNIER & PETERSEN (1991). It occurs in muddy sediments, from silt to muddy sand; with the exception of the Spanish Basque coast, where it may be found at depths of about 100 m, *C. pygodactylata* usually inhabits shallow waters between 1 and 30 m.

Unlike the former species, *C. soyeri* is sometimes considered as a cosmopolitan species. It is basically known from the Western Mediterranean — French and Spanish Catalan coast (LAUBIER, 1963, 1965; REYSS, 1971; DESBRUYÈRES *et al.*, 1972), Gulf of Lions (this study), Tyrrhenian Sea (GAMBI & GIANGRANDE, 1986), Adriatic (COGNETTI-VARRIALE & ZUNARELLI-VANDINI, 1978) — where it occurs in muddy bottoms, at depths between 12-35 m, but also up to 1,000 m (REYSS, 1971). The re-examination of specimens collected by EWING (1984) confirms its occurrence in the Northern Gulf of Mexico, in fine sediments at depths of 21-189 m. Additional records (not examined because the collections could not be located) of *C. soyeri* include several locations in the Celtic Sea — 610-1,400 m (AMOUREUX, 1982) — , in the Bay of Biscay — Galician rias (LOPEZ-JAMAR, 1982; LOPEZ-JAMAR & MEJUTO, 1986); Banc Le Danois, 450-1,500 m (AMOUREUX, 1987) —, and off Portugal – 320-1,040 m (AMOUREUX, 1987) –; these records need to be confirmed by collecting new specimens.

Specimens collected in Ensenada Harbour, Baja California, Mexico and referred to *C. soyeri* by SALAZAR VALLEJO & DONATH HERNANDEZ (1984) were anterior fragments with the dorsal tentacle arising from the posterior margin of setiger 2. Unfortunately, these specimens became dried during storage. We examined some dried worms, labelled "*C. soyeri*", from a neighbouring location; the worms were impossible to determine but, in one of them, the tentacle was clearly inserted on the anterior margin of setiger 3 as in *C. candida* Hartman collected from the same area and also re-examined. It is hypothesized that cossurids from the Mexican Pacific coast with the dorsal tentacle on setiger 2 might be *C. pygodactylata* rather than *C. soyeri*.

Another disconcerting record of *C. soyeri* is that of ROSENFELDT (1989) in the central Red Sea at 601 m depth. The single specimen was an anterior end of 41 setigers, 1.5 mm [sic] long. No detail is given about the dorsal tentacle or the number of thoracic setigers, so this record is doubtful.

In conclusion, the geographical distribution of *C. pygodactylata* is extended to the entire Pacific coast of North America and to both sides of the northern Atlantic, whereas *C. soyeri* appears to be restricted to the Mediterranean Sea and the northern Gulf of Mexico. Such a latitudinal distribution of these two species in the Atlantic seems ecologically justified, whereas the extended distribution of *C. pygodactylata* on the Pacific coast from California to Washington is more difficult to explain. It is also clear that the very few morphological characters available to distinguish these two species do not strengthen this conclusion. From this point of view, it would be desirable to confirm the morphological results using genetical methods of species identification.

## ACKNOWLEDGEMENTS

I. MADANI, X. de MONTAUDOUIN, J.L. CRABOS, P.J. LABOURG and G. OLLIVIER are thanked for their assistance in the field. R. LE MENN, Département de Microscopie, Université de Bordeaux I, is also gratefully acknowledged for preparing the specimens and SEM micrographs. Thanks are extended to the following persons and institutions for providing material or unpublished information: Michel BHAUD and Jean-Michel AMOUROUX, Laboratoire Arago (LA), Banyuls-sur-Mer, France; Kristian FAUCHALD, National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., USA; Jean-Claude DAUVIN, Muséum National d'Histoire Naturelle (MNHN), Paris, France; Florencio AGUIRREZBALAGA and Carlos SOLA, Sociedad Cultural INSUB, San Sebastian, Spain; Peter E. GIBBS, Plymouth Marine Laboratory, UK; Alex MUIR, British Museum (Natural History) (BMNH), London, UK; Sergio I. SALAZAR VALLEJO, Centro de Investigaciones de Quintana Roo, Chetumal, Mexico; Arturo H. ARIÑO, Universidad de Navarra, Pamplona, Spain; Luis E. CALDERON AGUILERA, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Mexico; Ana RALLO, Universidad del Pais Vasco (UPV), Bilbao, Spain. We are also very indebted to Judith A. FOURNIER, Canadian Museum of Nature, Ottawa, for helpful comments on earlier drafts and encouragement.

## REFERENCES

AGUIRREZABALAGA, F., 1984. — Contribución al estudio de los Anélidos Poliquetos de la Costa de Guipúzcoa. *Munibe, San Sebastian*, **36** : 119-130.

Source : MNHN, Paris

AGUIRREZABALAGA, F., ALTUNA, A., BORJA, A., FELIU, J., GARCIA-CARRASCOSA, A.M., ROMERO, A., SAN VICENTE, C., TORRES-GOMEZ-DE-CADIZ, J.A., URIZ, M.J. & IBAÑEZ, M., 1984. — Contribución al conocimiento de la fauna marina de la Costa Vasca II. *Lurralde*, **7** : 83-133.

AMOUREUX, L., 1982. — Annélides Polychètes recueillies sur la pente continentale de la Bretagne à l'Irlande, campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre espèces nouvelles pour la science. II. Inventaire taxonomique annoté de toutes les Polychètes sédentaires. *Cah. Biol. mar.*, **23** : 179-214.

AMOUREUX, L., 1987. — Annélides Polychètes du talus continental européen. Données complémentaires concernant les campagnes 1970 - 1971 - 1972 de la "Thalassa". Données globales sur l'ensemble des six campagnes (1967 à 1973). *Cah. Biol. mar.*, **28**: 569-577.

BANSE, K., 1963. — Polychaetous annelids from Puget Sound and the San Juan Archipelago, Washington. *Proc. Biol. Soc. Wash.*, **76**: 197-208.

BANSE, K., 1981. — On some Cossuridae and Maldanidae (Polychaeta) from Washington and British Columbia. *Can. J. Fish. Aquat. Sci.*, **38** : 633-637.

BERKELEY, E. & BERKELEY, C., 1956. — Notes on Polychaeta from the east coast of Vancouver Island and from adjacent waters, with a description of a new species of *Aricidea*. *J. Fish. Res. Bd. Canada*, **13** : 541-546.

BOUCHET, J.M., 1968. — *Etude océanographique des chenaux du Bassin d'Arcachon*. Thèse Doctorat, Université de Bordeaux, 2 vols., 163 + 306 pp.

COGNETTI-VARRIALE, A.M. & ZUNARELLI-VANDINI, R., 1978. — Distribution des Polychètes sur les fonds meubles infralittoraux du Molise (Adriatique). *Cah. Biol. mar.*, **19** : 37-45.

CURTIS, M.A., 1977. — Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. *Ophelia*, **16** : 9-58.

CURTIS, M.A., 1979. — A list of benthic polychaetes from Godhavn, West Greenland, with remarks on new records for Greenland. *Astarte*, **12** : 1-3.

DAUVIN, J.C. & GENTIL, F., 1980. — Nouvelles espèces pour l'inventaire de la faune marine de la région de Roscoff : Annélides Polychètes et Crustacés Amphipodes. *Trav. Stat. Biol. Roscoff (N.S.)*, **26** : 5-10.

DAY, J.H., 1963. — The polychaete fauna of South Africa. Part 8: New species and records from grab samples and dredgings. *Bull. Brit. Mus. (Nat. Hist.), Zool.*, **10** : 383-445.

DAY, J.H., 1967. — A monograph on the Polychaeta of Southern Africa. Part 2. Sedentaria. *Trustees Brit. Mus. (Nat. Hist.)* : 459-878.

DESBRUYÈRES, D., GUILLE, A. & RAMOS, J.M., 1972. — Bionomie benthique du plateau continental de la côte catalane espagnole. *Vie Milieu*, **23** : 355-366.

EWING, R.M., 1984. — Chapter 4. Family Cossuridae Day, 1963. *In*: J.M. UEBELACKER, & P.G. JOHNSON (eds), *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico*. Barry A. Vittor & Associates, Inc., Mobile, Alabama, **4** : 1-6,.

EWING, R.M., 1987. — Review of the genus *Cossurella* (Polychaeta: Cossuridae) including descriptions of two new species and a key to the species of the world. *Bull. biol. Soc. Wash.*, **7** : 3-10.

FAUCHALD, K., 1972. — Polychaetous annelids from deep water off western Mexico and adjacent areas in the Eastern Pacific. *Allan Hancock Monogr. Mar. Biol.*,**7** : 1-520.

FAUCHALD, K. & JUMARS, P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. Ann. Rev.*, **17** : 193-284.

FOURNIER, J.A. & PETERSEN, M.E., 1991. — *Cossura longocirrata* : redescription and distribution, with notes on reproductive biology and a comparison of described species of *Cossura* (Polychaeta : Cossuridae). *Ophelia*, Suppl. **5** : 63-80.

GAMBI, M.C. & GIANGRANDE, A., 1986. — Distribution of soft-bottom polychaetes in two coastal areas of the Tyrrhenian Sea (Italy): structural analysis. *Estuar. Cstl Shelf Sci.*, **23** : 847-862.

GARDINER, S.L. & WILSON, Jr., W.H., 1977. — New records of polychaete annelids from North Carolina with the description of a new species of *Sphaerosyllis* (Syllidae). *J. Elisha Mitchell Sci. Soc.*, **93** : 159-172.

GIBBS, P.E., 1969. — A quantitative study of the polychaete fauna of certain fine deposits in Plymouth Sound. *J. mar. biol. Ass. U.K.*, **49** : 311-326.

Source : MNHN, Paris

HARTMAN, O., 1954. — The marine annelids of San Francisco Bay and its environs, California. *Allan Hancock Foundation Occ. Pap.*, **15** : 1-20.

HARTMAN, O. 1955. — Endemism in the North Pacific Ocean, with emphasis on the distribution of marine annelids, and descriptions of new or little known species. *In*: *Essays in the Natural Sciences in Honor of Captain Allan Hancock on the Occasion of his Birthday*. University of Southern California Press, Los Angeles : 39-60.

HARTMAN, O., 1969. — *Atlas of the Sedantariate Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.

HARTMAN, O., 1976. — Polychaetous annelids of the Indian Ocean including an account of species collected by members of the International Indian Ocean Expeditions, 1963-64 and a catalogue and bibliography of the species from India. *J. mar. biol. Ass. India*, **16** : 191-252.

HOBSON, K.D. & BANSE, K., 1981. — Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Can. Bull. Fish. Aquat. Sci.*, **209** : 1-144.

JONES, M.L., 1956. — *Cossura pygodactylata*, a new annelid from San Francisco Bay (Polychaeta: Cirratulidae). *J. Wash. Acad. Sci.*, **46** : 127-130.

LAUBIER, L., 1963. — Découverte du genre *Cossura* (Polychète, Cossuridae) en Méditerranée: *Cossura soyeri* sp.n. *Vie Milieu*, **14** : 833-842.

LAUBIER, L., 1965. — Quelques Annélides Polychètes de l'Atlantique récemment signalées ou nouvelles en Méditerranée occidentale. *Rapp. P.-v. Réun. Commn int. Explor. scient. Mer Méditerr.*, **18** : 135-138.

LOPEZ-JAMAR, E., 1982. — Distribución espacial de las comunidades bentonicas infaunales de la Ría de Arosa. *Bol. Inst. Esp. Oceanogr.*, **7** : 255-268.

LOPEZ-JAMAR, E. & MEJUTO, J., 1986. — Evolución temporal de cuatro comunidades infaunales submareales de las Rías de Arosa y Muros. Resultados preliminares. *Bol. Inst. Esp. Oceanogr.*, **3** : 95-110.

MADANI, I., 1989. — *Dynamique des populations et processus de recrutement chez quatre espèces de Bivalves appartenant aux genres* Abra *et* Cerastoderma, *dans le Bassin d'Arcachon*. Thèse Doctorat, Université de Bordeaux I. 152 pp.

MONTAUDOUIN, X. de, 1988. — *Etude quantitative et qualitative de la macrofaune benthique des chenaux du Bassin d'Arcachon*. D.E.A. Océanologie, Université de Bordeaux I, 22 pp. (unpubl. report).

ORENSANZ, J.M., 1976. — Los anélidos poliquetos de la provincia biogeográfica Argentina. IX. Poecilochaetidae y Cossuridae. *Comunic. Zool. Mus. Hist. Nat. Montevideo*, **10** : 3-8.

RALLO, A., 1988. — Anélidos poliquetos recogidos en la plataforma litoral vizcaina (Golfo de Vizcaya, Atlántico Oriental). I. Résultados taxonomicos. *Cuad. Invest. Biol. (Bilbao)*, **13** : 135-143.

REISH, D.J., 1958. — Description of a new species of *Cossura* (Annelida: Polychaeta) from the Mississippi Delta. *J. Wash. Acad. Sci.*, **48** : 53-55.

REYSS, D., 1971. — Les canyons sous-marins de la Mer catalane, le Rech du Cap et le Rech Lacaze-Duthiers. III. Les peuplements de macrofaune benthique. *Vie Milieu*, **22**(3B): 529-613.

ROSENFELDT, P., 1989. — Die Polychaeta der Rotmeer - Expeditionen MESEDA I (1977) mit FS "Sonne" und MESEDA II (1979) mit FS "Valdivia". *Senckenbergiana Biol.*, **69** : 213-242.

SALAZAR VALLEJO, S.I. & DONATH HERNANDEZ, F.E., 1984. — Primer registro para México y extensión de rango de *Cossura soyeri* Laubier, 1964 (Annelida: Polychaeta). *Ciencias Marinas (Méx.)*, **10** : 61-67.

SOLA, J.C. & IBAÑEZ, M., 1986. — Estudio de la fauna de Anélidos Poliquetos de los fondos blandos del Estuario del Bidasoa. *Lurralde*, **9** : 165-181.

SPECHT, A., 1988. — Chaetae. *In*: W. WESTHEIDE & C.O. HERMANS (eds), The Ultrastructure of Polychaeta. *Microfauna Marina*, **4** : 45-59.

THULIN, G., 1921. — Biologisch-faunistische Untersuchungen aus dem Öresund. VI. Über *Cossura longocirrata* Webster und Benedict und über die Röhren von *Disoma multisetosum* Oersted. *Lunds Universitets Årsskrift, N.F.*, **2** : 2-15.

WEBSTER, H.E. & BENEDICT, J.E., 1887. — The Annelida Chaetopoda from Eastport, Maine. *U.S. Commission of Fish and Fisheries. Part 13. Report to the Commissioner for 1885* : 707-755.

Source : MNHN, Paris

Source : MNHN, Paris

# Larvae-substrate relationships of *Eupolymnia nebulosa* (Montagu, 1818) (Polychaeta, Terebellidae): an experimental analysis

*Michel BHAUD & Jae Hoon CHA*

Observatoire Océanologique de Banyuls, Université P. et M. Curie
et Unité Associée au CNRS
Laboratoire Arago, 66650 Banyuls-sur-mer, France

ABSTRACT

The transition from the plankton to the benthos has been investigated experimentally with a terebellid annelid. Tests on artificial and natural sediments lead to the following results. 1) Larvae were able to displace particles with a greater weight than their own, but this was possible only if larvae had access to a perfectly immobile platform. Larvae required two kinds of substrate for settlement, one forming support, the other for building the tube. 2) Mechanisms of the substrate selection by larvae do not suppose a "choice" from several sediments presented at the same time and equally accessible; larvae were either able to use the particles which they contact or unable to do so, in which case they returned to the water column. These tests indicated more an ecological opportunity than a choice. 3) The reduced selectivity of larvae with age corresponded to an increasing ability to use particles. Larvae, at each stage of development, were able to manipulate only a well defined size range of particles. This range increased as development proceeded, and the result was the progressive utilisation developing in the direction of increasing grain sizes. 4) Selection of sediment by larvae was accomplished on the short term and did not assure the future of individuals. The result of the transition from the planktonic to the benthic phase was unrelated to the subsequent success or failure of recruitment. A contrast became visible between limited requirements in terms of grain size and shape defining a large potential zone for larval settlement, on the one hand, and a spatially limited adult area, on the other hand. These two features were made compatible by the existence of an egg mass in the life cycle.

RÉSUMÉ

**Relations larves-substrat chez la polychète térébellide *Eupolymnia nebulosa* (Montagu, 1818): analyse expérimentale**

La transition plancton/benthos a été analysée expérimentalement sur une annélide polychète térébellide. Les tests réalisés sur des substrats artificiels et naturels ont conduit aux résultats suivants. 1) Les larves sont capables de déplacer des particules d'un poids supérieur à leur propre poids; cela est rendu possible par l'accès des larves à un point d'appui parfaitement immobile. A l'échelle des larves, la fabrication du premier tube benthique nécessite deux catégories dimensionnelles de particules: les unes constituant le support et les autres les éléments du tube. 2) Les mécanismes d'établissement des larves sur un substrat ne reposent pas sur un choix entre plusieurs sédiments présentés simultanément et également accessibles. Les larves peuvent ou non, utiliser les particules qu'elles contactent et dans le cas négatif, elles retournent dans la colonne d'eau pour préparer un

BHAUD, M. & J.H. CHA, 1994. — Larvae-substrate relationships of *Eupolymnia nebulosa* (Montagu, 1818) (Polychaeta, Terebellidae): an experimental analysis. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 371-381. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

nouveau test. Cette succession d'essais indépendants traduit une opportunité écologique et non un choix. 3) L'apparente diminution de sélectivité avec l'âge représente une augmentation des capacités d'utilisation des particules par les larves. A chaque stade de développement, elles manipulent une gamme de taille bien définie qui s'élargit avec l'âge; le résultat est une utilisation progressive vers les tailles élevées d'un sédiment hétérogène. 4) Les larves sélectionnent le substrat sur un court terme en fonction de leur capacité de manipulation. Elles n'assurent pas nécessairement la réussite des stades ultérieurs. Un contraste apparaît entre d'une part les faibles exigences granulométriques des larves conduisant à définir une large zone potentiellement favorable à leur fixation et d'autre part la zone de présence des adultes particulièrement réduite. Ces deux éléments sont rendus compatibles par la présence d'une structure de rétention des larves dans le cycle de vie.

## INTRODUCTION

A study was undertaken in the Bay of Banyuls in order to determine the factors influencing the composition and maintenance of benthic communities. Recruitment success has been discussed as an important process regulating communities. Larval behaviour, predation, local hydrodynamic patterns and substrate characteristics were the most frequently cited factors controlling larval settlement (ECKMAN, 1983; BUTMAN, 1986; WATZIN,1983). Several hypotheses have been presented to explain the long term structure of communities. From reaction patterns of first contact, active habitat selection has been suggested as opposed to passive deposition (BUTMAN, 1987). Habitat selection (MEADOWS & CAMPBELL, 1972) was proposed along with ecological opportunity (MOORE, 1975). In this second pair of hypotheses, the local distribution of adults was viewed as largely determined by selection of larvae. Other field observations supported the hypothesis of constrained settlement, i.e., this pattern resulted in a local distribution determined more by availability of suitable sites than by selection between equally accessible alternatives. These hypotheses, which are based on field observations, are probably not as conflicting as suggested by MOORE (1975); they must be tested in the laboratory. We approached this problem by using *Eupolymnia nebulosa,* Polychaeta. In the Bay of Banyuls, *E. nebulosa* is one of the most abundant species for which a large body of biological information is available. Its life cycle has been described (BHAUD & GREMARE, 1988, 1991) and preliminary experimental studies investigating settlement requirements have also been done (BHAUD, 1990b; CHA & BHAUD, 1991).

## MATERIAL AND METHODS

EXPERIMENTAL DESIGN. — Four types of experiments were conducted (Table 1) to answer the following questions: what kind of sediments separately presented are larvae able to use? If they are able to use a given sediment, how does this ability vary with larval age and increasing particle size? What is the behaviour of larvae when offered a variety of sediments including unsorted heterogeneous sediments, artificial or natural sediments ?

1) The initial experiments were conducted to determine whether or not the larvae had the ability to use a particular sediment. Sediments of various nature, size, settling velocity and organic matter content were tested. One type of sediment was placed in a separate glass petri dish 9 cm in diameter. Rates of larval settlement were determined after four days. During preliminary experiments (BHAUD, 1990a & b) we had observed that a heterogeneously distributed sediment of variable thickness resulted in more tubes being present on the margins of the dish where the sediment layer was thinner. The number of introduced larvae was approximately 300; the percentage of free larvae was calculated after counting 100 larvae with or without tubes, at five places chosen at random but avoiding the margins. Free larvae were classified as those swimming or lying on the bottom; in the latter case, no tube has been constructed .

2) To test the effects of larval age on the ability to use a given sediment, 14-day old and 18-day old larvae were introduced into an aquarium containing either a series of sediments consisting of microbeads (MB), or decanted silt (DS) (Table 2, items 7 and 8, respectively), each available as a thin (t) or thick (T) layer. Four plates were tested in an aquarium, and each paired aquaria represented a replicate. Sediments were deposited in each aquarium on plates of equal surface area. The number of tubes on each test sediment in an aquarium, counted after four days, was expressed as a percentage of the total number present on all sediments of this aquarium.

3) To test the ability to use different sized grains of one sediment, 14 day old larvae were tested in sediments consisting of fractions of the fine sand in a range of eight degrees of fineness. Oservations were made daily on each sediment for six days.

4) In an earlier study (CHA & BHAUD, 1991), and in experiment number 2 (present paper), a greater number of larvae settled in thin layers of sediment, whether it was mud or microbeads, than in thick layers of sediment. It was

Source : MNHN, Paris

suggested that access to a hard substrate, as a result of the thin layer of sediment, facilitated settlement. To complement the earlier findings on the role of a heterogeneous substrate, larvae were offered two types of sediment combined in three substrates: decantation silt (DS, Table 2: no 8) in a thick or a thin layer, and a fraction of Fontainebleau sand (160-200 µm; Table 2: no 3) with traces of DS (approximately in the ratio 1/500). Only one enclosure was provided with 3x5cm plates in alternate positions. In addition to these perfectly sorted sediments, two natural sediments were also tested: the silty sand from the *Nephtys hombergii* community and the fine sand from the *Spisula subtruncata* community.

**Supply of larvae**. — Larvae were obtained from egg masses (BHAUD, 1990a) which were maintained in a tank 60 cm (l) x 40 cm (w) x 16 cm (h) filled with 50 litres of filtered sea water. Filtering was achieved by passing the water through synthetic fiber-wool. The water was circulated at a rate of 0.5 l /min using a flow-through system, the surface water was drained away by an overflow. When larvae were close to hatching from the mucoid mass, they were removed to a one litre vessel and gently agitated. After 2 hours, the emerged larvae were transfered to a second vessel with filtered sea water. Larvae were used either immediately or kept for several days until the desired developmental stage was reached. Estimates of numbers were made from a subsample obtained by immersing a tube of known diameter in the vessel containing larvae and gently agitating to obtain a homogeneous suspension (RAZOULS, 1972). A range of 500 to 60,000 larvae were collected from one egg mass with an average of about 5,000 larvae. They were collected from late February to early June.

Two methods of collecting larvae of varying age were used. a) Newly produced egg masses were collected at particular intervals and maintained at the same temperature; b) Egg masses were divided and each half was incubated at a different temperature. Development was shortened by 6 days when the temperature was increased from 12 to 18 °C for eight days.

**Morphology of larvae introduced into enclosures**. — Morphology and age were calculated from a known time-development series determined at the beginning of the reproductive season in March (BHAUD, 1988a). Growth rate was positively correlated with temperature (BHAUD, 1988b). Larvae of five setigerous segments in March is 14 day-old but is only eight day-old in early June. This variation in rate of larval development was minimized by characterizing the larvae by morphology rather than by age. The date of each experiment was recorded in the course of the reproductive period. Experiments were conducted in March. Larvae measured 430 to 510 µm in length in experiments 1, 2, 3 and 4; they had five setigers, each with one pair of provisional club-shaped setae and the first 4 setigers with one pair of capillary setae. They were 14 days old. A second group of larvae, also used in experiment 2, had eight setigers, each with one pair of provisional club-shaped setae, and the first six setigers with one pair of capillary setae. They were 18 days old.

**Criteria for settlement**. — Settlement success was measured by the appearance of the primary tubes of juvenile benthic stages. This method ensured that the number of tubes counted represented the number of animals present in the sediment. Counts were verified by inspecting all tubes under a binocular microscope for the presence of living, dead or abandoned tubes. All larvae built tubes and never abandoned them in these short experiments. Mortality was negligible. The change from planktonic to benthic life was not a cause of mortality (BHAUD & CHA, 1992). In order to confirm that we would be able to find dead larvae, 10 larvae with six setigerous segments, were sacrificed (repeated three times). These dead larvae were still recognizable six days later. This confirmed the absence of dead larvae at the time of observations made four days after the introduction of larvae.

**Feeding**. — It was not necessary to feed these larvae during these experiments since they still had yolk reserves present in their digestive tract after eight days (CHA, 1990, BHAUD, 1991).

**Duration of experiments**. — Our study was designed to explore the behaviour of larvae at the time of settlement and the interaction between settling larvae and natural and artificial sediments. Settlement involved behaviour indicative of the benthic life stage (BUTMAN, 1987) and was defined as the first lasting contact with the bottom (KEOUGH & DOWNES, 1982). Tube building was used as an indication that settlement had occurred. The distribution of larvae was determined among several substrates four days after the introduction of larvae (Experiments 1, 2 and 4). However, this did not exclude daily observations, allowing us to register intermediate steps and in particular provisionally settled larvae as in experiment 3.

**Sediment type**. — The following sediments were used in one or more of the experiments. Mud obtained by sedimentation from the laboratory running sea-water supply (decantation silt: DS) then sieved through 40 and 60 µm mesh. Fontainebleau sand (FS) (Prolabo, France) was composed of grains between 100 and 315 µm in diameter. This sand was separated according to the following diameters: 100 to 160 µm, from 160 to 200 µm, from 200 to 250 µm, and from 250 to 315 µm. An artificial sediment was used (Ferro Prod., Cataphote division, USA) with microbead sizes measuring 45 to 60 µm and 100 to 150 µm. A second artificial sediment of equal sized

Source : MNHN, Paris

Pyrex particles (OSI, France) was used. Two natural sediments from Banyuls Bay were used: a) silty sand from the *Nephtys hombergii* community which was composed of 5 to 20 % clay (< 40 µm), 50 to 80 % fine sand (> 40 µm and < 200 µm) and less than 5 % of medium-sized sand (> 200 µm); b) fine sand from the *Spisula subtruncata* community which was composed of 5-10 % clay, 80-90 % fine sand and 5-10 % medium-sized sand. A fraction > 40 and < 63 µm of these natural sediments (NH and SS for *Nephtys hombergii* and *Spisula subtruncata*) was isolated and the settling rate compared with that of the other sediments. All sediments used are reported in Table 2 with the following characteristics: size, shape, sinking velocity and ability of larvae to use sediments.

TABLE 1. — Main features of the experimental design. Number of sediments used in one experiment is related to the nature of particles; number of substrates used in the same experiment is deduced from the pattern of presentation (thick or thin layer, sorted or not sorted...); replicates are given by the number of aquaria, even if several equivalent supports are present in one aquarium; S= sediment.

| Exp. Nb | 1: Table1. | 2: Fig.1. | 3: Fig.2. | 4A: Table 3 | 4B: BHAUD & CHA, 1992 |
|---|---|---|---|---|---|
| Questions asked | capability to manipulate | influence of age on the ability to manipulate particles | | importance of heterogeneous particles | relation with field communities |
| | grains of a defined size | 2 age classes face to several S | 1 age classe face the size range of 1 S | | |
| Nb of sediments (S) | 14 | 2 | 1 | 2 | 2 |
| thick (T) or thin (t) layer | T | T t | T | Tt | T |
| Nb of substrates to which larvae have access | 1 | 4 | 8 | 3 | 2 (with large range size) |
| homogeneous (hm) or hete-rogeneous (ht) grain size | hm | hm | hm | hm+ht | ht |
| choice given | no | yes: in a space larger than the perceptive volume of the larvae | | | yes: inside the perceptive volume of the larvae |
| Nb of replicates | 2 | 10 | 1 | 1 | 10 |
| Nb of supports for substrate in each aquarium | 1 | 2 | 1 | 5 | 5 |
| incubation (days) | 4 | 4 | 1 to 6 | 4 | 4 |
| observation at the end of incubation period (E) or each day | E | E | ED | E | E |
| age (days) of introduced larvae | 14 | 14+18 | 14 | 14 | 14 |
| higher distance between centre of two adjoining supports (cm) | - | 12 | 16 | 12 | - |

Among well-sorted sediments, only decanted silt (items 8 and 9 in Table 2) has some organic content (1.13 mg. $g^{-1}$ dry weight of organic material) and probably also a large amount of microbial biomass; these elements are known to be strongly correlated with the surface area of the particles (DEFLAUN & MAYER, 1983). Previous experiments (BHAUD, 1990a, b) have shown that the suitability of a substrate was not correlated with the relative or absolute quantity of organic matter, which suggested the importance of physical characteristics of sediment for larval settlement.

Characteristics of the sediments may have changed during experiments if their introduction into sea water was made at the beginning of the experiment, just before adding the larvae. Sediments were prepared in filtered sea water one week before use in enclosures with the same water to avoid the possibility of a sudden development of microfauna.

Source : MNHN, Paris

TABLE 2. — Sinking velocity and preference for several sediments types by larvae of *E. nebulosa*. The ability of these larvae to use the sediment and to construct or attempt to construct tubes is assigned a value from 0 (grains not displaced) to ++++ (well constructed tubes). F S: Fontainebleau sand; MB: microbeads; DS: decantation silt; PY: Pyrex; SS: fine sand of *Spisula subtruncata* community; NH: silty sand of *Nephtys hombergii* community. Observations four days after introduction of larvae. Origin is either synthetic product (S) or a natural product (N). Sediments were sorted in sea water (sw) with a silk plankton net or sorted in dried conditions (dc) with a metallic sieve or the size range directly furnished (df). In the column "shape", is given the ratio of longitudinal to transverse axis. The different levels of the use of sediments (observed in two replicates) have been photographed and presented elsewhere (CHA & BHAUD, 1992). Free larvae are live larvae, in the water column or on the sediment but without attached particles. S: sediment.

| sediment | | origin | sorting methods | fall velocity | | shape | ability to use sediment | observations |
|---|---|---|---|---|---|---|---|---|
| item | D µm | | | $cm.s^{-1}$ | SD(N=6) | | | |
| 1 F S | 250-315 | N | d c | 3.034 | 0.039 | | 0 | no marks of bioturbation;100 % living and free larvae. |
| 2 F S | 200-250 | N | d c | 2.752 | 0.035 | approximately spherical or weakly | 0 | no marks of bioturbation; 100 % living and free larvae. |
| 3 F S | 160-200 | N | d c | 2.340 | 0.038 | elongated (1/2) smooth angles | + | clusters of some grains appearing; 100 % living and free larvae. |
| 4 F S | 100-160 | N | d c | 1.270 | 0.003 | | ++ | clear arrangement of grains in linesbut structure of tube inconspicuous; 70 and 76 % of free larvae. |
| 5 F S | 40-60 | N | d c | 0.358 | 0.002 | | +++ | structure of tubes evident; 25 and 35 % of free larvae. |
| 6 M B | 105-150 | S | d f | 0.855 | 0.003 | perfectly spherical | +++ | structure of tubes evident, 20 and 28 % of free larvae |
| 7 M B | 45-60 | S | d f | 0.390 | 0.001 | and smooth | ++++ | very fine tubes of good appearance, perfectly built, very long and in relief; 6 and 10 % of free larvae |
| 8 D S | 40-60 | N | s w | 0.462 | 0.003 | mineral part + | ++++ | perfectly built tubes, appearing in prominent position relatively to the surface of the sediment; no free larvae |
| 9 D S | < 40 | N | s w | 0.199 | 0.000 | organic part | ++++ | same observations. |
| 10 PY | 40-60 | S | d c | 0.240 | 0.000 | variable shape, never spherical, sharp angles and sharp edges | + | structure of tubes inconspicuous; arrangement of particles only in short lines (1mm); numerous tracks without larvae; 92 % and 45 % of larvae inside sediment but not in built structures. |
| 11 PY | < 40 | S | d c | 0.180 | 0.000 | same as above | +++ | structure of tubes evident (3cm); 60 % and 35 % of larvae in tubes; other larvae are free; no tubes built then deserted |
| 12 NH | < 63 | N | s w | 0.428 | 0.002 | mineral + organic part | ++++ | perfectly built tubes. |
| 13 SS | 40-63 | N | d c | 0.210 | 0.003 | approximately spherical or weakly elongated (1/2) sharp angles | ++++ | same observations. |
| 14 PC | < 10 | N | d f | 0.178 | 0.008 | microplates | 0 | no tube; 100 % living and free larvae |
| 15 | Larvae from same eggmass | | | 0.110 | 0.012 | 12 day-old living specimens | | values obtained using 30 individuals for each of the 10 fall observations in each age group. |
| | | | | 0.115 | 0.028 | 14 day-old living specimens | | |
| | | | | 0.105 | 0.017 | 16 day-old living specimens | | |

**Preparation of sediments.** — Supports of sediments were set out on the bottom of aquaria. These were movable plates allowing for easy manipulation (CHA, 1990). Sediments were deposited with a pipette onto these

Source : MNHN, Paris

plates in thick or thin layers. Thick layers were 1 and 2 µm thick, which prevented the larvae from reaching the bottom of the movable plates, and thin layers were one to two layers of particles (approximately 120-300 µm), which allowed the larvae to reach the surface plates and thus could be considered as a hard substratum.

**Speed of sediment deposition**. — Sinking sediment was timed in a test chamber 42 cm high and 6.5 cm in diameter. The chamber was filled with seawater having a salinity of 37.58 ‰, and the temperature maintained at 18 °C. The settling velocity was calculated from Stokes' Law:

$$V = r^2C, \text{ with } C = \text{constant, or } V = (D/2)^2 \times 2(d_1-d_2)g / 9 z d_2$$

with D: diameter of grains, $d_1$: density of the particle, $d_2$: density of water, g: gravitational acceleration, z: kinematic viscosity of the fluid (BUCHANAN, 1971). The vessel was placed in a controlled temperature room and surrounded by plastic plates disposed on four sides and on the top. For measuring rate of descent of the particles, the lower part of one side was open in order to observe the particles reaching the bottom. A drop of dye was added and observed to establish that temperature gradients did not exist.

**Hydrodynamic conditions**. — All experiments were conducted in aquaria measuring 60 x 40 x 20 cm containing still sea water 15cm deep. In this set up, the distribution of tubes could only arise from the larvae's ability to move. Larvae made multiple passes over the plates; visits of these plates were followed by a return to the water column, after leaving a mark on the sediment. Light and temperature were similar for all experiments.

**Observation of larvae**. — Larvae were observed at the surface of the sediment using two compound microscopes: one with a horizontal line of sight, the other with a vertical line of sight. These two microscopes were set on supports equipped with rollers which enabled them to travel on two long horizontal guides (CHA, 1990).

**Quality of the biological materials**. — Spawned egg masses were available in large numbers which permitted the use of large volumes in contrast to "finger bowl" ecology (SCHELTEMA, 1986). The synchrony of development within one egg mass provided individuals at the same developmental stage. The egg masses were laid in the field. The success of settlement was recorded by counting the number of tubes present. Tube building did not stop once it had commenced. All larvae appeared healthy and the number of live individuals did not change significantly during the experiments in spite of a change from pelagic to benthic ecosystems.

## RESULTS

**Manipulation of particles by larvae with no choice of sediment**. — (exp. nb. 1 in Table 1). Table 2 shows that the maximum particle size for transport and agglomeration was about 160 µm. The optimal particle size for construction of a clearly defined individual tube was 60 µm. The use of sediment seemed to be related to the ease with which the particles could be manipulated. There was an inverse correlation between the sedimentation rate of particles and the ability of the larvae to manipulate particles and construct a tube. Sedimentation rates of live larvae were also measured as for the sediments. For 12 to 16 day old larvae, the mean, of 30 trials, (Table 2: n° 15) was one-half that for the finest silt particles (n° 9) and one-fourth that of the larger silt particles (n° 7 and 8). Items 7, 8 and 9 were the most used particles.

Comparison of the net weight of larvae and particles may explain these results. Net weight is given by 6 z ($d_1$-$d_2$) V D/2. Larvae are viewed as spheres of 120 µm D, and are compared to sediment 7 (Table 2) which contained the larger particles (D= 60 µm) used in tube construction. All parameters giving net weight were known except for $d_1$; however, the density of organic matter of larvae was certainly lower than that of the sediments and ($d_1$-$d_2$) is thus lower for larvae. If Dlarvae is twice Dsediment, and Vlarvae is four times lower than Vsediment, the net weight of larvae is one-half that of the sediment. The problem of manipulating particles arises from the fact that the net weight of the larvae is lower than the particles. Under these conditions how may larvae grasp particles? We observed that for sediments 1-5, and for 6-7 (each group with same $d_1$), strength of use grew when D and V decreased, or when net weight of particles decreased. That suggested that use of particles by larvae was correlated with the weight of particles.

**Effect of larval age**.— (exp. nb. 2 in Table 1). Two stocks of larvae (14 and 18 day old, respectively) were presented (Fig. 1) with two types of sediments (microbeads, MB and decanted silt DS, items 7 and 8 in Table 1) with each sediment presented as a thick and a thin layer. Each experiment was run in two enclosures, each enclosure receiving one age class and four substrates. Ten replicates were carried out. Only a summary is given with the quantitative data reduced as the percentage of the total number of tubes in each of the four sediments. Younger larvae preferred the thin layer of sediment. Presence (in DS) or absence (in MB) of organic matter was not a source of variance. The greatest difference which occurred between the highest and lowest number of tubes

Source : MNHN, Paris

was 41.8 and the coefficient of variation was 88.2. The nature and the thickness of the sediment were of lesser importance for the old larvae than for younger. The greatest difference in the number of settled larvae was only 22.5 % with a coefficient of variation of 47.1. A comparison test ($\chi^2$) of the two series gave a significant difference at a confidence level of 0.05. An age difference of four days resulted in highly modified settlement. Older larvae were less susceptible to differences between substrates; they had a settlement capability greater than younger larvae, and they were distributed more evenly between different sediments.

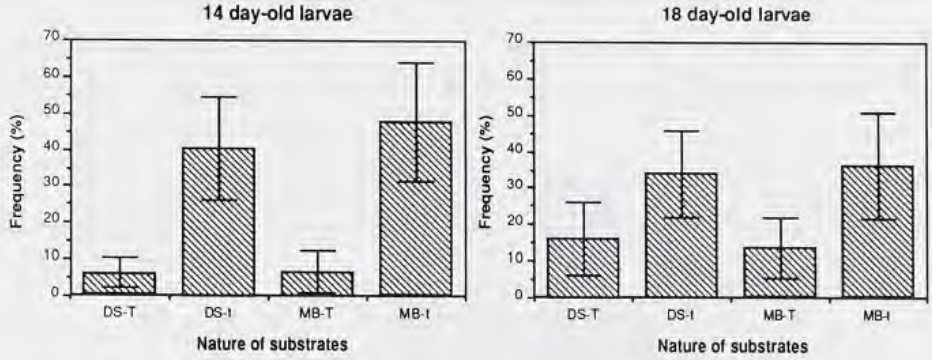



FIG. 1. — Effect of larval age on selectivity with four sediments, as shown by comparing settlement on various sediments by larvae 14 (left) and 18 (right) days old. Blocks represent the percentage of the number of tubes which appeared after 4 days for each age group in each series of four sediments. Mean from 10 replicates. Vertical bars represent standard deviations. DS: decanted silt < 60 µm; MB: microbeads 60-45 µm; T: thick layer; t: thin layer.

**Effect of duration of incubation**. — (exp. nb. 3 in Table 1). Approximately 2,000 larvae were introduced into an enclosure with eight size fractions of fine sand from the *S. subtruncata* community. The numbers of tubes constructed were observed daily, and these data are summarized in figure 2. Twenty-four hours after the introduction of larvae, the rates of settlement were highest on the finer sediments (1, 2 and 3), lower on middle-grade ones (4 and 5) with no settlement on the coarser ones (6, 7 and 8). Sediments of grades 1 and 2 were the preferred substrate on day 6. Sediments of grade 4 had a similar number of tubes as grade-3 sediment after six days, but they appeared later. Very few tubes were made in sediment grades 6, 7 and 8 and they were not formed until day 6.

Addition of tubes formed on each sediment grade was normalized to 100 (Fig. 2), but the number of tubes built on each sediment was not the same. Comparison of the real number of settled larvae on substrates just after disappearing from the water column (horizontal boxes "hrs2"), with the number of tubes counted on day 6 (horizontal boxes "day 6"), allows one to conclude that a numeric rearrangement occurs. Larvae settling on sediment 6-7-8 cannot use it but can still return to the water column. This increased the probability of reaching easy to use sediments. A small fraction of larvae visiting 6-7-8 and registered in boxes "hrs2" do not leave these sediments. They can wait for several days during which morphological development proceeds. Accordingly, unused sediment on the first day may be used four or six days later. On sediments 4 and 5, tubes appeared only on the third day. Sediments most easily manipulated at the start of the experiment had the highest density of tubes at the conclusion. Larvae which sedimented on sediment 1-2-3 had the opportunity to settle and did not leave.

**Use of heterogeneous sediments**. — (exp. nb. 4 in Table 1). The preceding experiments 1 to 3) were not directly relevant to the Bay of Banyuls where sediments are more or less heterogeneous. The most homogeneous sediment (the Well Sorted Fine Sand) is formed of 70 % of 100 to 200 µm particles plus a small fraction of larger (200 to 500 µm) and smaller (< 40 µm) particles (GUILLE, 1970). We used natural calibrated sediments, isolated or mixed together, and two natural, unsorted sediments in reconstructing natural sediments for laboratory experiments.

a) *Natural sediment, artificially sorted.* — The larvae were offered three sediments with five replicates each and were placed in one aquarium. The number of tubes were counted at day four. Treatments were randomly distributed. The three sediments were: (a) silt in thick layer giving a very fluid boundary layer, (b) silt in thin

Source : MNHN, Paris

layer, (c) sand in thick layer with a thin layer of silt on the surface. Statistical comparison (Table 3) showed that a & b, and a and c, were significantly different but treatments b and c were not.

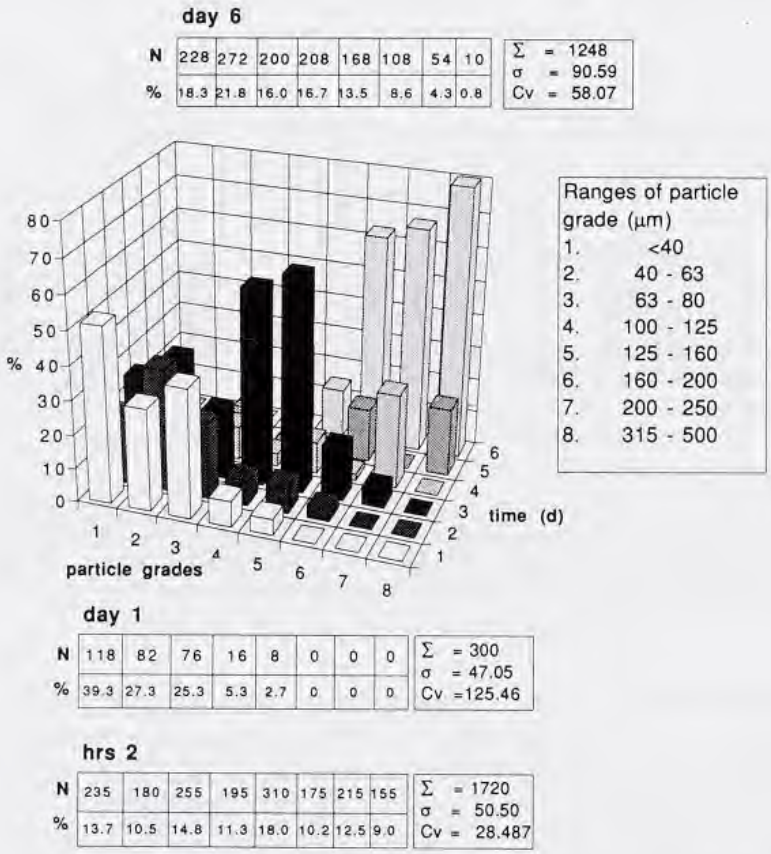



FIG. 2. — Rates of tube-building by 14-day-old larvae of *E. nebulosa* in different fractions of sand from the *Spisula subtruncata* community. For each sediment grade, blocks give the number of newly built tubes, per day. The block values in each sediment add up to 100. In fact, the number of tubes built on each sediment is not constant; the real situations for days 1 and 6 are given in horizontal boxes, below and above, respectively. The reordering is deduced from comparison of horizontal boxes "hrs 2" (distribution of larvae without tube, two hours after their introduction) and horizontal boxes "day 6" (juveniles in tube, no larvae without tube).

A grain of sand 160-200 µm in diameter was too large for tube building (Table 1). The tubes in series c were made from silt but not from the sand. The difference in colour between silt and sand made the grey silt tubes conspicuous against the white sand (CHA & BHAUD, 1992). These results suggest that conditions for settlement were similar in b and c: the material used to build tubes in both cases was silt and the large grains of sand, in c, were not used. To explain these observations, we examined the larvae in detail under a compound microscope.

This experiment suggested that a solid base is necessary for aggregation of particles with mucus by larvae and for positioning larvae as the tube is built. Construction seemed to be impossible on a fluid substrate which continually gives way and contained no solid components. This explained why the results from treatments b and c were similar as large sand grains in c acted as stable bases for settlement, similar to the bottom of dishes in treatments b.

b) *Natural sediments.* — The larval requirements for settlement, as identified by the preceding experimental observations, allow one to predict which natural sediments are suitable for juveniles of *E. nebulosa*. Juveniles required a minimum of clay and medium-sized sand grains. The silty sand of the *N. hombergii* community seems

Source : MNHN, Paris

suitable, as well as the fine sand of the *S. subtruncata* community. Experiments confirmed that these sediments were potential substrates for *E. nebulosa* larval settlement. In each of 10 replicates, 50 larvae introduced into enclosures with these two natural substrates produced 50 formed tubes and inhabited by well-developed juveniles. The important result was demonstrating the ability of the larvae to use a fraction of a heterogeneous sediment. Photographs and additional results have been presented elsewhere (CHA & BHAUD, 1992).

TABLE 3. — Number of tubes distributed among three substrates, each presented on five plates in one aquarium; surface of plates 63 $cm^2$. ANOVA shows that total means are significantly different from each other, which justifies comparisons in pairs showing that b and c are not different.

| sediment | thickness of the layer | mean | ANOVA | Scheffe F. Test |
|---|---|---|---|---|
| a DS (< 60 µm) | thick | 197 | F. test: | a-b: 13.58* |
| b DS (< 60 mm) | thin | 410 | 15.726 | a-c: 9.68* |
| c sand (160-200 µm) | thick layer + thin layer of DS | 377 | p: 0.0004 | b-c: 0.329 |
| | | | | * significant at 0.05 level |

## DISCUSSION AND CONCLUSIONS

The four groups of experiments described provided information concerning several aspects of larval settlement: (1) the need for a heterogeneous substrate, (2) the importance of the age of larvae at the time of first contact with the sediment, and (3) the mechanism of substrate selection. Sediment preferences may change as larvae increase in size and age. This may not be applicable to other species; a behavioural variability may occur (RAIMONDI & KEOUGH, 1990).

A solid settlement base is required for coordinated movements of the animal. These coordinated movements assume that the compression of the coelomic fluid, permitting extension of the body, is possible. The manipulation and arrangement of particles is then possible. This dual constraint (solid base plus manipulable building particles) is related to the nature of the substrate. It differs from previous conclusions which suggested that only grain size was important for settlement (WILSON, 1948, 1952 for *Ophelia bicornis*; GRAY, 1967 for *Protodrilus rubropharyngeus*; DORSET, 1961 and HEMPEL, 1957 for *Polydora ciliata*). Our experiments show also the importance to settlement of the thickness of the layer of sediment. Similar observations have been made for *Polydora ciliata* (LAGADEUC, 1991) and *Thelepus setosus* (DUCHÊNE, 1983). WILSON (1952), among the 29 points of his summary, and BUTMAN (1987), in her review, did not approach this question.

Larvae at each stage of development are able to manipulate only a well-defined size range of particles. This range increases as development proceeds. The older the larvae are when they touch the substratum for the first time, the weaker their ability to return to the water column if the substrate is unsuitable. In the same way, the suitable particle size range increases with age, and the probability of successful settlement increases. These behavioural modifications are probably very frequent during development. They are linked to the morphological development by the increasing number of tentacles, setigers and oncinial plates in *E. nebulosa*. These modifications have also been observed in molluscs (AABEL, 1983, 1984; LABOURG & LASSERRE, 1980).

The mechanism of substrate selection is dependent upon whether the larvae can use a particular particle or not. In this context it is possible to refer settlement to opportunity rather than choice. A choice supposes a comparative action on a small time and space scale between equally and simultaneously accessible alternatives. Opportunity results from tests developed by larvae faced with only a single sediment size present.

Application of experimental results to the life cycle of *E. nebulosa* under natural conditions is limited. Experimental work on *E. nebulosa* settlement can only be partially transferred to the field. Larvae were able to settle on two natural sediments: the fine sand and silty sand of *S. subtruncata* and *N. hombergii* communities, respectively. However, juveniles have not been collected from these sediments during a one year study of the Bay of Banyuls (GREHAN, pers. comm.) nor in epibenthic sledge samples collected two months after the first spawning period (BHAUD & CHA, pers. obser.). Adults have not been found in soft substrates in the Bay of Banyuls (GUILLE, 1970). Adult habitat requirements of *E. nebulosa* suggest that their absence in both the *N. hombergii* and the *S. subtruncata* communities is not surprising. Adults of *E. nebulosa* are collected among rhizomes of the seagrass *Posidonia* in Banyuls (KERNEIS, 1960). LAUBIER (1966) stated that *E. nebulosa* is present in low numbers on coralline substrates on the French Mediterranean catalan coast. This species also occurs on algae of the upper part of the infralittoral level, on the "silty coastal bottoms" and in the Lacaze-Duthiers canyon (LAUBIER & PARIS,

Source : MNHN, Paris

1962). A detailed study in the English Channel (LANG, 1986) showed that individuals were protected by boulders buried in the sediment; their tubes were located on the lower side of the boulders, in close contact with the sediment. Thus, *E. nebulosa* is a species that lives at the interface of hard and soft substrate. Heterogeneity of substratum is acknowledged as a requisite for settlement of larvae and points to the way of life of adults. While larvae can settle on a variety of substrates, these may not be able to support adult populations. The presence of egg masses restricts the dispersal of larvae, and larval retention represents the coordination between two elements of the life cycle: modest granulometric requirements defining a large potential area for settlement, and a spatially limited adult distribution. The mucous structure makes these two elements compatible by limiting larval dispersal.

## ACKNOWLEDGEMENTS

This work is a contribution to the French National Program on the Determinism of Recruitment (PNDR) and was supported by a grant to the authors from IFREMER and CNRS. Special thanks go to P. HUTCHINGS, D. REISH and S. v. BOLETZKY for their comments on the manuscript and improvements of the English text.

## REFERENCES

AABEL, J.P., 1983. — Morphology and function in post-metamorphal *Abra alba* (Bivalve, Tellinacea). *Sarsia* , **68** : 213-219

AABEL, J.P., 1984. — The effect of development of the inhalant siphon on growth rate of juveniles *Abra alba* (Wood) (Bivalvia: Tellinacea). *Sarsia*, **69** : 87-89.

BHAUD, M., 1988a. — Influence of temperature and food supply on development of *Eupolymnia nebulosa* (Montagu, 1818) (Polychaeta, Terebellidae). *J. Exp. Mar. Biol. Ecol.*, **118** : 103-113.

BHAUD, M., 1988b. — Change in setal pattern during early development of *Eupolymnia nebulosa* (Polychaeta: Terebellidae) grown in simulated natural conditions. *J. mar. biol. Assoc. U.K.*, **68** : 677-687.

BHAUD, M., 1990a. — Conditions d'établissement des larves de *Eupolymnia nebulosa*: acquis expérimentaux et observations en milieu naturel. *Oceanis*, **16** : 181-190.

BHAUD, M., 1990b. — Acquisition de la vie benthique par *Eupolymnia nebulosa* (Polychète Terebellidae): dispositifs expérimentaux et premiers résultats. *Vie Milieu*, **40** : 17-28.

BHAUD, M., 1991. — Larval release from the egg mass and settlement of *Eupolymnia nebulosa* (Polychaeta, Terebellidae). *Bull. mar. Sci.*, **48** : 420-431.

BHAUD, M. & GRÉMARE, A., 1988. — Larval development of the terebellid polychaete *Eupolymnia nebulosa* (Montagu, 1818) in the Mediterranean Sea. *Zool. Scr.* , **17** : 347-356.

BHAUD, M. & GRÉMARE, A., 1991. — Reproductive cycle of *Eupolymnia nebulosa* (Polychaeta, Terebellidae) in the western Mediterranean sea. *Ophelia* , suppl. **5** : 295-304.

BHAUD, M. & CHA, J.H., 1992. — Sources de fluctuation et de stabilité dans le déroulement du cycle de vie de *Eupolymnia nebulosa* en Méditerranée. *Ann. Inst. Océanogr.*, **68** : 25-35

BUCHANAN, J.B., 1971. — Measurements of the Physical and Chemical Environment. Sediments. *In:* N.A. HOLME & A.D. McINTYRE (eds), Methods for the study of Marine Benthos. *IBP Handbook*, **16** : 30-58.

BUTMAN, C.A., 1986. — Larval settlement of soft-sediment invertebrates: some predictions based on an analysis of near-bottom velocity profiles. *In*: J.C. NIHOUL (ed), *Marine Interfaces Ecohydrodynamics, Oceanography Series*, **42**, Elsevier : 487-513.

BUTMAN, C.A., 1987. — Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol. Annu. Rev.*, **25** : 113-165.

CHA, J.H., 1990. — *Les conditions d'établissement des larves de la polychète* Eupolymnia nebulosa *(Montagu) dans un canal hydrodynamique*. D.E.A., Océanol. Biol., Université Paris VI. Rapport de stage : 47 pp.

CHA, J.H. & BHAUD, M. , 1991. — Etude expérimentale du recrutement benthique en canal hydrodynamique et en milieu calme. *C.R.Acad.Sci.Paris*, (313) **3** : 113-118.

Source : MNHN, Paris

CHA, J.H. & BHAUD, M., 1992. — *The Terebellid Polychaete* Eupolymnia nebulosa *(Montagu, 1818); Experimental analysis of larvae-substrate relationships in development of the life cycle*. ECSA-ERF Conference, Plymouth: 13th-18th September 1992

DEFLAUN, M.F. & MAYER, L.M., 1983. — Relationships between bacteria and grain surfaces in intertidal sediments. *Limnol. Oceanogr.*, **28** : 873-881

DORSETT, D.A., 1961. — The behaviour of *Polydora ciliata* (Johnst.). Tube-building and burrowing. *J. mar. biol. Assoc. U.K.*, **41** : 577-590.

DUCHÊNE, J.C., 1983. — Développement larvaire et fixation chez *Thelepus setosus* (Annélide Polychète) à Kerguelen, Province subantarctique. *Vie Milieu* , **33** : 65-77.

ECKMAN, J.E., 1983. — Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.*, **28** : 241-257.

GRAY, J.S., 1967. — Substrate selection by the archiannelid *Protodrilus rubropharyngeus*. *Helgol.Wiss. Meeresunters.*, **15** : 253-269.

GUILLE, A., 1970. — Bionomie benthique du plateau continental de la côte catalane française. II: les communautés de la macrofaune.*Vie Milieu*, **21** : 149-280.

HEMPEL, C., 1957. — Über den Röhrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta sedentaria) der deutschen Küsten. *Helgol. Wiss. Meeresunters.*, **6** : 100-134.

KERNEIS, A., 1960. — Contribution à l'étude faunistique et écologique des herbiers de Posidonies de la région de Banyuls. *Vie Milieu* , **11** : 145-187.

KEOUGH, M.J. & DOWNES, B.L., 1982. — Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia*, **54** : 348-352.

LAGADEUC, Y., 1991. — La vase à *Polydora ciliata* (Johnston, 1828), annélide polychète: origine et influence sur la fixation des larves. *Cah. Biol. mar.*, **32** : 439-450.

LANG, F., 1986. — *Peuplement des fonds durs du Bassin de la Rance; rôle fonctionnel de Eupolymnia nebulosa (Annélide Polychète)*. Thèse Doct., Univ. Rennes I, 240 pp.

LABOURG, P.J. & G. LASSERRE, 1980. — Dynamique des populations de *Cerastoderma glaucum* dans une lagune aménagée de la région d'Arcachon. *Mar. Biol.*, **60** : 147-157.

LAUBIER, L., 1966. — Le coralligène des Albères. Monographie biocénotique. *Ann. Inst. Océanogr. Monaco*, Paris , **43** : 137-316.

LAUBIER, L. & PARIS, J., 1962. — Faune marine des Pyrénées-Orientales. Fas.c 4: Annélides Polychètes.*Vie Milieu*, **13** : 1-81.

MEADOWS, P.S. & CAMPBELL, J.I., 1972. — Habitat selection by aquatic invertebrates. *Adv. Mar. Biol.*, **10** : 271-361.

MOORE, P.G., 1975. — The role of habitat selection in determining the local distribution of animals in the sea. *Mar. Behav. Physiol.*, **3** : 97-100.

RAIMONDI, P.T. & KEOUGH, M.J., 1990. — Behavioural variability in marine larvae. *Austral. J. Ecol.*, **15** : 427-437.

RAZOULS, C., 1972. — *Estimation de la production secondaire (Copépodes pélagiques) dans une province néritique méditerranéenne (Golfe du Lion)*. Thèse doct. Etat, Sci. Nat., Univ. Paris VI., 1, 301pp.

SCHELTEMA, R.S., 1986. — On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bull. mar. Sci.*, **39** : 290-322.

WATZIN, M.C., 1983. — The effects of meiofauna on settling macrofauna: meiofauna may structure macrofaunal communities. *Oecologia*, **59** : 163-166.

WILSON, D.P., 1948. — The relation of the substratum to the metamorphosis of *Ophelia* larvae. *J. mar. biol. Assoc. U.K.*, **27** : 723-760.

WILSON, D.P., 1952. — The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* Savigny. *Ann. Inst. Océanogr.*, Paris, **27** : 49-156.

Source : MNHN, Paris

Source : MNHN, Paris

# Is *Owenia fusiformis* Delle Chiaje a cosmopolitan species ?

*Jean-Claude DAUVIN* *& *Eric THIÉBAUT* **

*Muséum national d'Histoire naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie
URA CNRS 699, 57, rue Cuvier 75231 Paris Cedex 05, France
**Observatoire Océanologique, Université P. & M. Curie, Paris VI et CNRS-UPR 4601
B.P. 74, 29682 Roscoff, France

ABSTRACT

Some works on Polychaetes report that a very large fraction of the class is widely distributed with a large bathymetric range. Nevertheless, several recent studies have shown limited distribution of species or genus in the world; it has also been questioned whether or not any "cosmopolitan" polychaete species exists as a single species. The tube-building polychaete *Owenia fusiformis* is considered to have a world wide distribution with depths ranging from shallow littoral to 4,554 m. However, geographical and bathymetric distribution of this species remains uncertain. The objective of this paper was to bring together all available data in order to present an up-to-date review of the knowledge on the genus *Owenia*. Moreover, some observations of macroscopic morphological characters (the presence of a thoracic collar and eye-spots, the structure of the tube) of specimens collected in Atlantic, Pacific and Indian Oceans were presented. From this study, only two species remain valid: *O. lobopygidiata*, which is a bathyal and abyssal Pacific species, and *O. fusiformis*. *O. collaris* described in the eastern Pacific and Carribean and *O. caudisetosa*, which was only known from the Salvador coasts, are junior synonyms of *O. fusiformis*. Although there is some variability of microscopic and macroscopic morphological characters, these variations do not allow for the identification of several species from *O. fusiformis* populations. *O. fusiformis* seems truly cosmopolitan which is absent only in Antarctic waters. It is a typical sandy and muddy-sandy species. The species is abundant only in shallows waters (0-40 m), but it is found with certainly to 2,325 m. The records from greater depths are doubtful insofar as the specimens are usually fragmented and may be reported as the bathyal species *O. lobopygidiata*. The species is able to develop different reproductive strategies in relation to latitude. Further work is necessary to complete the biological studies of populations especially from the coldest and warmest waters, and to investigate if there are isolated genetic populations.

RÉSUMÉ

***Owenia fusiformis* Delle Chiaje est-elle une espèce cosmopolite ?**

Chez les Polychètes, de nombreux travaux ont mis en évidence une prépondérance d'espèces possédant une large répartition géographique et bathymétrique. Toutefois, des études récentes ont remis en cause ce cosmopolitisme, divisant

DAUVIN, J.C. & E. THIEBAUT, 1994. — Is *Owenia fusiformis* Delle Chiaje a cosmopolitan species ? *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 383-404. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

les espèces largement distribuées en plusieurs espèces distinctes. L'annélide polychète tubicole *Owenia fusiformis* est une de ces espèces avec une distribution géographique étendue ; elle est présente des eaux littorales aux zones abyssales, jusqu'à 4554 m. Toutefois, cette répartition demeure incertaine. L'objectif de cet article est de présenter une synthèse de l'ensemble des données recueillies sur le genre *Owenia*. De plus, les résultats d'observations de caractères morphologiques macroscopiques (présence d'une collerette thoracique et de taches oculiformes, structure du tube) de spécimens récoltés dans les océans atlantique, pacifique et indien sont présentés. Deux espèces demeurent valides : *O. lobopygidiata*, présente dans les zones pacifiques bathyales et abyssales et *O. fusiformis*. *O. collaris*, décrite dans l'est Pacifique et les Caraïbes et *O. caudisetosa*, décrite et signalée uniquement sur les côtes du Salvador doivent être considérées comme synonymes d'*O. fusiformis*. *O. fusiformis* semble donc être une véritable espèce cosmopolite, absente seulement de l'Océan Antarctique. Caractéristique des sédiments sableux et sablo-vaseux, elle est abondante uniquement dans les eaux côtières (0-40 m) et trouvée avec certitude jusqu'à 2325 m. Les signalisations plus profondes sont douteuses dans la mesure où les spécimens récoltés sont rarement entiers et peuvent se référer à l'espèce abyssale *O. lobopygidiata*. *O. fusiformis* est capable de développer différentes stratégies reproductives en fonction de la latitude. A l'avenir, il est nécessaire de (1) compléter les études de biologie des populations, principalement dans les eaux froides et tropicales et (2) tester si les différentes populations sont génétiquement séparées.

## INTRODUCTION

FAUVEL (1959) reported that there are no biogeographical regions for the polychaetes. Available data on the polychaetes confirm that a very large fraction of the class is widely distributed or with a large bathymetric range (HOLTHE, 1978). Nevertheless, several studies show limited distribution of the species or genus in the world wide ocean (WELLS, 1963; KNIGHT-JONES *et al.*, 1991). The tube-building polychaete *Owenia fusiformis* Delle Chiaje is reported to have a world wide distribution from low-water mark to 4,554 m (HARTMAN, 1965). Howewer, the geographical and bathymetric distribution of *O. fusiformis* is uncertain as it is questionable whether any "cosmopolitan" polychaete species is a single species (NILSEN & HOLTHE, 1985). Since the beginning of the century, a large geographical distribution of the species was cited by GRAVIER (1906). The objective of this paper is to bring together all available data in order to present an up-to-date review of bathymetry, ecological and geographical distribution, biology and morphology of *O. fusiformis*. This work is limited by several methodological problems such as: (1) most of the available data came from ecological studies which had not confirmed the species true identity; (2) many authors had just seen the tubes of *Owenia* and automatically referred them to *O. fusiformis* without examining the specimens. Therefore, in a preliminary work, to define the occurrence of one or more species of *Owenia*, some morphological characters of specimens from different localities of the Atlantic, Pacific and Indian oceans were examined.

## HISTORICAL

Although the synonymy of differents species was not always confirmed by the examination of type specimen, HARTMAN (1959) considered six valid species of *Owenia* in her catalogue:

***Owenia artifex*** (Verrill, 1885). *Ammochares artifex* VERRILL, 1885: 439.

***Owenia fusiformis*** Delle Chiaje, 1841; *Owenia fusiformis* Delle Chiaje, 1841: 31. *Ammochares aedificator* ANDREWS, 1891: 296, pl. 14, figs 42-45. *Ammochares assimilator* CAULLERY, 1944: 49 [error for *A. aedificator* Andrews, 1891]. *Ammochares assimilis* SARS, 1851: 201. MALMGREN, 1867: 210, pl. 12, fig. 65. *Ammochares ottonis* GRUBE, 1846: 164, pl. 5, fig. 2. *Ops digitata* CARRINGTON, 1865: 187. *Owenia assimilis* LEVINSEN, 1883: 148. WOLLEBAEK, 1912: 30, pl. 1, fig. 6 *Owenia brachycera* MARION, 1876: 312. *Owenia filiformis* -CLAPAREDE, 1868: 446, pl. 26, fig. 5.*? Ammochares brasiliensis* HANSEN, 1882: 19, pl. 5-6, figs 33-36, 1-4. *? Ammochares occidentalis* (JOHNSON, 1901 : 420, pl. 14, figs 140-142. *? Ammochares sundevalli* KINBERG, 1867 : 343 *? Ammochares tegula* KINBERG, 1867: 343.

***Owenia collaris*** Hartman, 1955. *Owenia fusiformis collaris* Hartman, 1955: 46, pl.2, figs 6-7. *Owenia collaris* HARTMAN, 1969: 493.

***Owenia lobopygidiata*** Uschakov, 1950. *Owenia lobopygidiata* Uschakov, 1950: 214, fig. 31. *Owenia lobopygidiata* USCHAKOV, 1955: 347, fig. 128 E-J.

Source : MNHN, Paris

***Owenia orientalis*** (Grube, 1878). *Ammochares orientalis* GRUBE, 1878 : 204, pl. 10, fig. 6.

***Owenia tenuis*** (Haswell, 1883). *Ammochares tenuis* HASWELL, 1883: 633, pl. 12, fig. 2.

Since Hartman's catalogue, only one species *Owenia caudisetosa* Hartmann-Schröder, 1959 has been described from Estero Jaltepeque, Salvador, Pacific. HARTMAN (1969) then raised *O. fusiformis collaris* Hartman, 1955 to specific rank as *O. collaris*, again clearly stating that *O. fusiformis* lacks a collar. FAUVEL (1953) gave *Ammochares orientalis* Grube, 1878 as a synonym of *O. fusiformis*. EHLERS (1901), then RULLIER (1965b) and DAY & HUTCHINGS (1979) considered *O. tenuis* (Haswell, 1883) as *O. fusiformis*. The species *Owenia artifex* (Verrill, 1885) from Cape Cod has not been cited since its description although many studies have been made in this region. This species is doubtful as its description corresponds to *O. fusiformis*; it is probably a synonym of *O. fusiformis*. From this summary, the genus *Owenia* would include four species: *O. caudisetosa, O. collaris, O. fusiformis* and *O. lobopygidiata.*

## MORPHOLOGICAL DIFFERENCES BETWEEN SPECIES

The principle morphological characters of *O. fusiformis* are: crown of tentacles projects forward from the head region, tentacular crown divided into two lobes, latero-ventral eye-spots, uncini with two teeth side by side, and pygidium with a pair of weakly developed lobes. DELLE CHIAJE (1841) did not indicate the presence of a collar in Mediterranean specimens. From primary description, the characters distinguishing the other species from *O. fusiformis* are: *O. lobopygidiata*, absence of ventral eye-spots and a pygidium with nine finger-shaped papillae; *O. collaris*, presence of a high, thoracic, membranous collar, and uncini with much longer teeth and without a shoulder; *O. caudisetosa*: small size, absence of ventral eye-spot and capillary setae on the first thoracic segment and the presence of one row of dark pigmentation at the branchial base. Three specimens of *O. caudisetosa* were examined. In contrast, with the original description these specimens have three thoracic segments with capillary setae. The presence of a pigmented row at the branchial base and the absence of eyes spots should not be considered as a specific character (see Table 1). All distinctive characters of this species are very similar to those of *O. fusiformis*, and the synonymy of the two species is proposed.

Table 1 gives the principle macroscopic morphological characters observed on specimens from several localities, including individuals from California named as *O. fusiformis collaris* and *O. collaris* by HARTMAN. A thoracic collar is present in all the individuals, but it is more or less developed. Specimens having a thickly developed collar are found on the American Pacific and Atlantic coasts, and Kuwait coast. On the North American coasts, there are specimens with or without a developed collar independent of latitude. On the contrary, on the European and African coasts, all the specimens have a smaller and thinner collar. The eye-spots are absent only in a few cases, but this may be due to preservation. A brown pigment band across a branchial lobes is present in specimens from the Senegal coasts (Table 1). MILLIGAN (1984) reported such brown pigmentation for individuals from the Gulf of Mexico. Different thorax pigmentation (one or two pigmented rows at the branchial base, or general pigmentation) are present principally on subtropical and tropical populations. The tube shows variable granulometric composition and arrangemen: grains of quartz and calcareous fragments piled like roof tiles or conglomerated sand grains or sand grains in a fibrous matrix. This tube structure seems to be related to the habitat of the worm. The pygidium does not vary in shape, and all specimens have three setigerous thoracic segments. Worms with a thick developed collar have a shorter branchial crown with the exception of Louisianan specimens which exhibit both short and long branchial crowns. In summary, this study shows that there is more intraspecific variability of some morphological characters than occurrence of several *Owenia* species. Since the thoracic collar occurs in specimens representing records from all parts of the world, the separation between *O. collaris* and *O. fusiformis* seems unjustified. Now, we consider that these two forms should be as *O. fusiformis*.

The number of segments and the number of uncini rows in each torus which were primarily used to distinguish *Owenia* species are correlated with age (THIÉBAUT & DAUVIN, 1992). SEM observations of uncini (THOMASSIN & PICARD, 1972; NIELSEN & HOLTHE, 1985; IMAJIMA & MORITA, 1987; GAMBI. 1989; THIÉBAUT & DAUVIN, 1992) from Mediterranean, Pacific, Atlantic and Indian populations, show a homogeneous shape to this character. THOMASSIN & PICARD (1972) have observed some differences between Mediterranean and Indian specimens; the two teeth arranged side by side do appear be at the same level for the Indian specimens. In summary, only two species known remain in the genus: *O. fusiformis* and *O. lobopygidiata.*

Source : MNHN, Paris

TABLE 1. — Morphological characters (thoracic collar, latero-ventral eye-spots, colouring of the thoracic region and tube structure) of *Owenia* specimens from different localities. N: number of observed specimens; n: number > 10; o : absent; * : present; * * : well developed. * identified as *Owenia collaris*. ** identified as *Owenia caudisetosa*.

| Locality | N | Collar | Eye-spots | Colouring | Tube |
|---|---|---|---|---|---|
| Bay of Seine (Fr.) | n | * | * | o | with calcareous fragments |
| N.E. Atl. - 10 m | | | | | piled like roof tiles |
| Bay of Morlaix (Fr.) N.E. Atl. - 17 m | n | * | o | o | with shell and calcareous fragments piled like roof tiles |
| Bay of Le Croisic (Fr.) N.E. Atl. | n | * | * | small pigmented area dorsally | with shell fragments and few sand grains piled like roof tiles |
| Bay of Prado (Fr.) Mediterranean Sea | n | * | * | o | with shell fragments and few sand grains piled like roof tiles |
| Salerno Gulf, Naples (It.) Mediterranean Sea, 4-10 m | n | * | * | dark area at the branchial base | with calcareous fragments and sand grains piled like roof tiles |
| North of Adriatic Sea (It.) Mediterranean Sea | 2 | * | * | pigmented row at the branchial base | with conglomerated sand grains |
| Po River Delta (It.) Mediterranean Sea -5 m | n | * | * | o | - |
| Bay of Alger (Alg.) Mediterranean Sea | n | * | * | small pigmented area dorsally | with calcareous fragments piled like roof tiles |
| Senegal coasts Tropical Atlantic | 2 | * | o | pigmented row in the branchial crown and a complete pigmented thorax | with calcareous fragments piled like roof tiles |
| Guinea coasts Tropical Atlantic | 1 | * | * | a complete pigmented thorax | with calcareous fragments piled like roof tiles |
| Ivory coasts Tropical Atlantic | 1 | * | * | a complete pigmented thorax | with calcareous fragments irregularly arranged |
| Benin coasts Tropical Atlantic | 2 | * | * | a complete pigmented thorax | with calcareous spicules |
| Newport (U.S.A.) | 2 | * * | o | o | with conglomerated sand grains |
| N.W. Atl. - 34 m | | | | | |
| Eastport (U.S.A.) N.W. Atl. | 1 | * | o | o | - |
| North Carolina (U.S.A.) N.W. Atl. - 29 m | 3 | * * | * | o | - |
| Indian River (U.S.A.) N.W. Atl. | 2 | * | o | o | with conglomerated sand grains and few calcareous fragments |
| Louisiane coasts (U.S.A.) N.W. Atl. -19.8 m | 6 | * * | o | o | with conglomerated sand grains and piled calcareous fragments |
| Panama coasts * Trop. Atl. | 1 | * * | * | two pigmented rows at the branchial base | with calcareous fragments piled like roof tiles |
| Brazilian coasts S.W. Atl. - 12 to - 63 m | 7 | * | * | variable coloration of branchial crown and thoracic region | with calcareous fragments |
| Alaska (U.S.A.) * N.E. Pac. | 2 | * * | * | o | with sand grains and calcareous fragments piled like roof tiles |
| False Bay (U.S.A.) N. E. Pac. | 3 | * | * | o | with sand grains piled like roof tiles |
| San Juan Islands (U.S.A.) N. E. Pac. | 2 | * | * | brown area on the thoracic region | with conglomerated sand grains |
| Puget Sound (U.S.A.) N. E. Pac. -23 m | 1 | * | o | o | – |
| Off California (U.S.A.) * N. E. Pac. - 93 m | 6 | * * | * | o | with conglomerated sand grains |

Source : MNHN, Paris

| Locality | N | Collar | Eye-spots | Colouring | Tube |
|---|---|---|---|---|---|
| Monterey Bay (U.S.A.) N.E. Pac. - 18 m | 1 | * | * | o | – |
| Tomales Bay (U.S.A.) * N.E. Pac. | n | * * | o | o | with sand grains piled like roof tiles |
| Santa Rosa Isl. (U.S.A.) * N.E. Pac. - 15 m | n | * * | * | o | with calcareous fragments piled like roof tiles |
| Santa Catalina I. (U.S.A.) * N.E. Pac. - 33 m | n | * * | * | o | with calcareous fragments piled like roof tiles |
| Salvador coasts ** N.E. Pac. | 3 | * | o | pigmented row in the branchial crown | - |
| Peruvian coasts S.E. Pac. - 34 m | n | * | * | pigmented points in the branchial crown and a pigmen-ted row at the branchial base | with some sand grains in a fibrous matrix |
| Off Kuweit N.W. Ind. | 1 | * * | * | o | with calcareous fragments piled like roof tiles |
| Jervis Bay (Austr.) S.W. Pac. | 8 | * | * | complete pigmented thorax | with calcareous fragments and sand grains piled like roof tiles |
| Hawkesbury (Austr.) S.W. Pac. | n | * | * | complete pigmented thorax | with conglomerated sand grains |

## ECOLOGICAL AND BIOLOGICAL CHARACTERISTICS

*O. fusiformis* is a typical soft-bottom species. It is found in a large granulometric spectrum from mud to coarse sand but it usually inhabits muddy sand/sandy sediments. In the English Channel, *O. fusiformis* is present only in bays and estuaries where fine sediments are confined in relation to low tidal currents (CABIOCH, pers. comm.). On the contrary, in the North Sea, *O. fusiformis* is widely distributed according widespread occurence of fine sediment (DEWARUMEZ, pers. comm.). On the Texas continental shelf, it is found in sandy sediment with a relatively low mud content (FLINT & RABALAIS, 1980).

*O. fusiformis* can feed in an upright position or bent over towards the substratum; thus it can be either a filter-feeder or surface deposit-feeder (FLINT & RABALAIS, 1980; GAMBI, 1989). It forms a crater around its tube, and it plays an important role in surface bioturbation (GAMBI, 1989). It is reported as a common prey for some flat fishes in the area where the population is dominant (EMMETT *et al.*, 1987; MÉNARD *et al.*, 1989).

The species can live three or four years in the English Channel. It is a polythelic polychaete, and only some specimens can reproduce at one year (MÉNARD *et al.*, 1989; GENTIL *et al.*, 1990). The effective fecundity is correlated with the length of the female which varies from 6,000 oocytes for a female of 40 mm in length to 85,000 oocytes for a female of 110 mm in length (THIÉBAUT & DAUVIN, 1991).

*Owenia* is known to produce a distinctive planktotrophic larvae (WILSON, 1932). In the Bay of Seine, English Channel, GENTIL *et al.* (1990) reported an annual reproductive cycle with a short summer sexual pause, a gonadial development during the autumn and spawning occurring from May to June. Recruitment occurred at the end of spring (DAUVIN, 1992). WILSON (1932) also reported mature adults from March to July with spawning in June in the Plymouth area. BHAUD (1972) compared his planktonic data from subtropical conditions (western Mediterranean) with results from boreal waters (southern Scandinavia). He showed a shorter occurrence of the mitraria larvae in northern waters (mid-June to mid-August) compared with southern waters (February to the end of June). CAZAUX (1973) reported the presence of larvae in planktonic samples from February to April in the Arcachon Bay. BUCHANAN *et al.* (1978) observed a marked summer recruitment in a population from the South Northumberland coasts, North Sea. These observations with an annual reproductive cycle are obviously different from those of Mc NULTY & LOPEZ (1969) who described a year-round breeding population in the subtropical waters of Biscayne Bay, Florida, but the life span is shorter in these warm waters. FAGER (1964) for a Californian population, which lives at least two years, observed a main spring recruitment, but also some new recruits through the year. In Disko Bay, West Greenland, *O. fusiformis* reproduced asexually by fragmentation and regeneration in the absence of favourable conditions for gametogenesis and spawning (CURTIS, 1977).

Source : MNHN, Paris

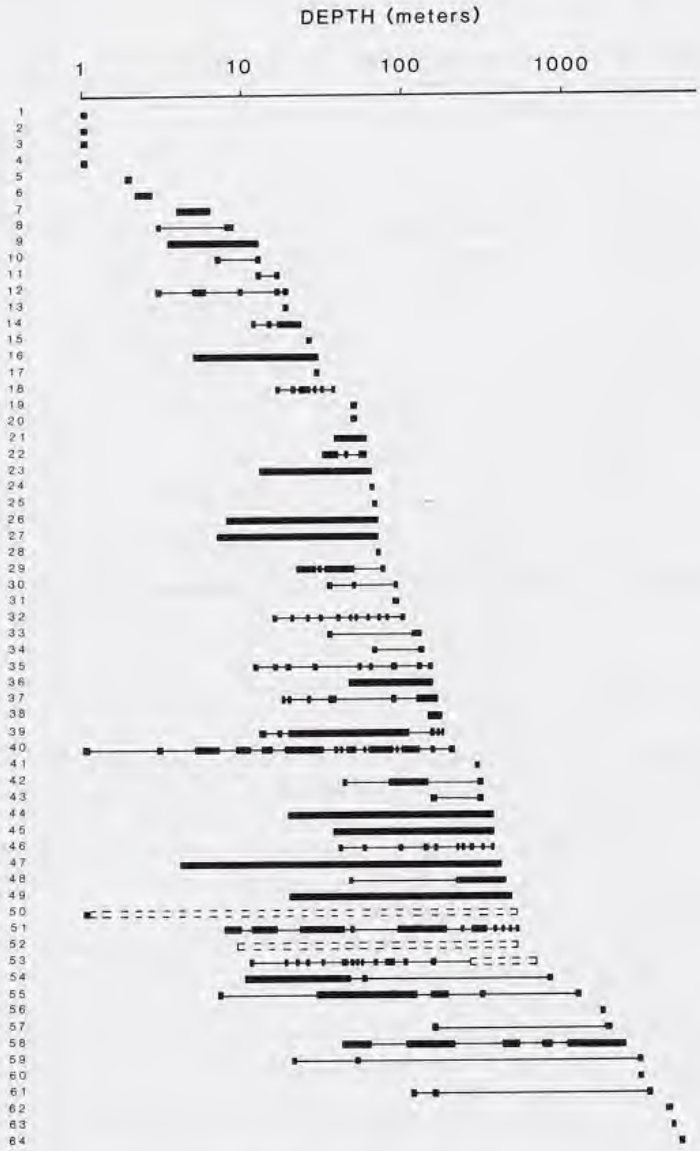



FIG. 1. — The bathymetric distribution of *O. fusiformis*. The thick line indicates effective depths of sampling, and the thin line the possible area of bathymetries. From: 1: AMOUREUX (1966), 2: ANDREWS (1891), 3: de SAINT JOSEPH (1898), 4: VOVELLE (1963), 5 : JELDES & LEFEVERE (1959), 6 : NICOLAIDOU *et al.* (1988), 7 : CAPACCIONI *et al.* (1991), 8: NICOLAIDOU & PAPADOPOULOU (1989), 9: COGNETTI-VARRIALE & ZUNARELLI-VANDINI(1979), 10: COGNETTI-VARRIALE& ZUNARELLI-VANDINI (1978), 11: GIANGRANDE & GAMBI (1986), 12 : GIBBS (1971), 13 : GEORGE (1974), 14: CHARDY *et al.* (1987), 15: FAUVEL & RULLIER (1959a), 16: WOLFF (1973), 17: GILLET (1985), 18: ELIASON (1962), 19: RULLIER (1965a), 20: HARTMANN-SCHRÖDER & HARTMANN (1965), 21: HARTMAN (1944b), 22: CLAVIER & GARRIGUE (1990), 23: RULLIER & AMOUREUX (1979), 24: BERKELEY & BERKELEY (1952), 25: IMAJIMA (1961), 26: WILLEY (1902), 27: BRUCE *et al.* (1963), 28: DUMITRESCO (1960), 29: MICHAELSEN (1897), 30 : FOURNIER & LEVINGS (1982), 3 : FAUVEL (1909), 32: INTÈS & LE LOEUFF (1977), 33: BELLAN (1969b), 34: IMAJIMA (1963), 35: DAY (1961), 36 : MILLIGAN (1984), 37: THÉEL (1879), 38: AMOUREUX (1973), 39: WESENBERG-LUND (1951), 40 : IMAJIMA & MORITA (1987), 41: FAUVEL(1911), 42: BIDENKAP (1907), 43: AMOUREUX (1972), 44: BIDENKAP (1894), 45: DANIELSSEN (1859), 46: HARTMANN-SCHRÖDER (1974a), 47: WOLLEBAEK (1912), 48: HARTMANN-SCHRÖDER (1986), 49: EHLERS (1875), 50: DAY (1967), 51: WESENBERG-LUND(1950b), 52: USCHAKOV (1955), 53: KIRKEGAARD (1959), 54: CAULLERY (1944), 55: MCINTOSH (1915), 56: KIRKEGAARD (1983), 57: WESENBERG-LUND (1950a), 58: BILYARD & CAREY (1979), 59: FAUVEL(1932), 60: HARTMAN (1966), 61: MCINTOSH (1879), 62: KIRKEGAARD (1980), 63: HARTMAN (1965), 64: ELIASON (1951).

Source : MNHN, Paris

TABLE 2. — Records of *Owenia* species at depths below 500 m. Condition of sampled individuals is given.

| DEPTHS (m) and SITES | AUTHOR | SAMPLE CONDITIONS |
|---|---|---|
| 500-1,366; Okhostsk Sea | USHAKOV (1955) | *O. lobopygidiata* |
| 775-3,225; Beaufort Sea | BILYARD & CAREY (1979) | no information |
| 798; Molucca Sea | CAULLERY (1944) | one worm named *O. fusiformis* but posterior part absent without pigmentation and no ventral eyespots: may be *O. lobopygidiata* |
| 1,152; N.E. Atlantic | McINTOSH (1915) | no information |
| 1,620-1,700; N.E. Atlantic | KIRKEGAARD (1983) | two specimens |
| 1,800; N.E. tlantic | WESENBERG-LUND (1950a) | 10 worms in tubes with few foraminiferan tests |
| 2,700; N.E. Indian | FAUVEL (1932) | only tubes with few foraminiferan tests |
| 2,725; Antarctic | HARTMAN (1966) | tube fragment only, as ? *Owenia* sp. |
| 3,213; N.W. Atlantic | McINTOSH (1879) | as *O. fusiformis*, only one tube fragment with foraminiferan tests |
| 4,120; N.E. Atlantic | KIRKEGAARD (1980) | one fragmentory worm as *O. ?fusiformis* |
| 4,250; N.E. Atlantic | KIRKEGAARD (14980) | five empty tubes as *O. ?fusiformis* |
| 4,554; N.W. Atlantic | HARTMAN (1965) | tubes covered with foraminiferan tests of *O. ?fusiformis* |
| 5,033-5,044; N.W. Atlantic | ELIASON (1951) | *Owenia* ? sp., fragments of tubes covered with foraminiferan test, with remnants of worm |
| 6,490-6,650; Banda Trench Indo-Pacific | KIRKEGAARD (1956) | ? *O. lobopygidiata*; fragments and tubes |
| 6,580; Banda Trench Indo-Pacific | KIRKEGAARD (1956) | ? *O. lobopygidiata*; one specimen and fragments |

## BATHYMETRIC DISTRIBUTION OF *OWENIA* SPECIES

*O. fusiformis* is found on the continental shelf 0-200 m (Fig. 1) with only 10 records exceeding 500 m and six 2,500 m. Few specimens are found depths greater than 500 m, and usually the animal is incomplete or only tube fragments are found. Most of reports citing *O. fusiformis* from below 500 m (Table 2) are not precise for the *O. fusiformis* status. These include: 1) tubes or tube fragments without worms but with foraminiferan tests proving the bathyal or abyssal origin; 2) identification with doubt as *O.? fusiformis* or *Owenia* ? sp. or ? *Owenia* sp.; and 3) incomplete worms that do not permit a specific identification. It is probable that many of the *Owenia* specimens found in deep water are *O. lobopygidiata*. The maximum depth of *O. fusiformis* appears to be 2,325 m in the Beaufort Sea (BILYARD & CAREY, 1979).

*O. lobopygidiata* is a western Pacific species present in Ohkotsk Sea and Bering Sea from 110 to 1366 m (USCHAKOV, 1955) and with doubts in the abyssal Banda Trench at 6,490-6,650 m (KIRKEGAARD, 1956).

## BIOGEOGRAPHICAL DISTRIBUTION OF *OWENIA FUSIFORMIS*

*Owenia fusiformis* occurs both sides of the Atlantic Ocean except along the north Brazilian coasts where the observations of polychaetes are limited (Fig. 2). In the eastern Atlantic, it has been observed from the north of Norway to South Africa. It is absent from the Baltic Sea. In the Mediterranean waters, it presents principally in the western part. It has been reported from the Bosphore in the Black Sea. In the western Atlantic, it is present from the Gulf of St Lawrence to Rio de la Plata, Argentina. In the Arctic, it is reported along both coasts of southern Greenland at 75 °N latitude. It reaches 80°N latitude, at Spitzberg Island and the New Zemble Island. It is also reported in the Kara Sea and the Beaufort Sea (Figs 2-3).

Source : MNHN, Paris

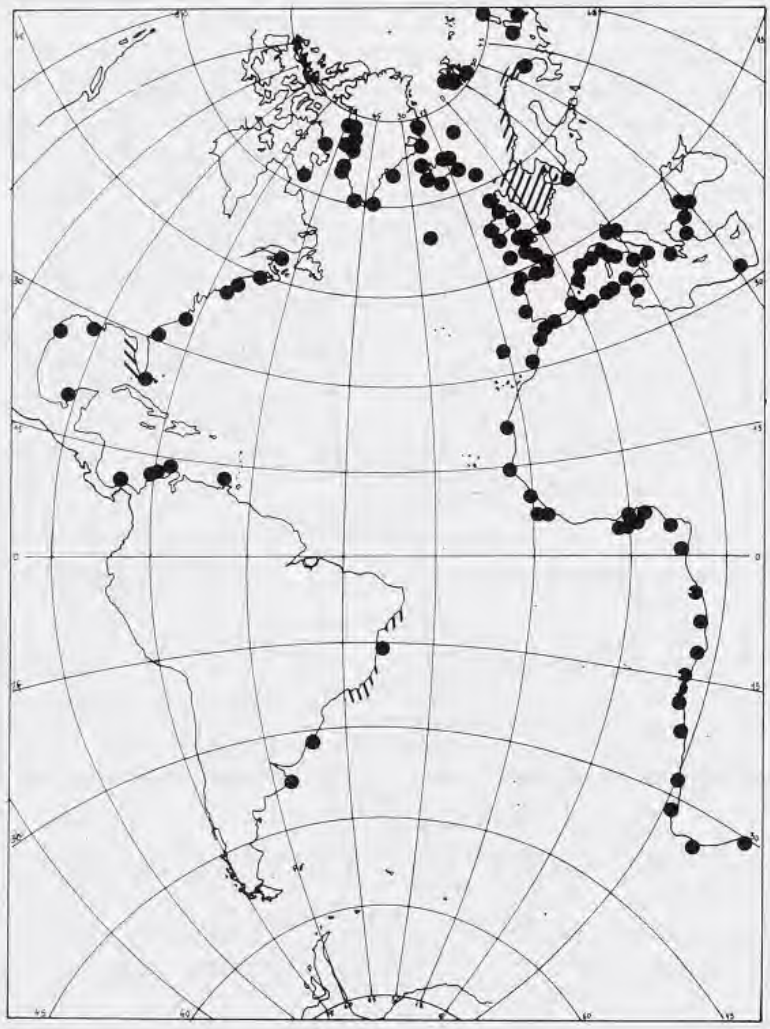


FIG. 2. — The atlantic distribution of *O. fusiformis*. From AMOUREUX (1966, 1970, 1971, 1972, 1973, 1976), ANADON (1980), ANDREWS (1891), AUGENER (1928), BACHELET (1981), BAKALEM & ROMANO (1978), BAKALEM (pers. comm.), BELLAN (1969a,b), BIDENKAP (1894, 1907), BRUCE *et al.* (1963), BUCHANAN (1957), BUCHANAN *et al.* (1978), CAPACCIONI -AZZATI *et al.* (1991), CASTELLI *et al.* (1991), CLAPARÈDE (1868), COGNETTI-VARRIALE & ZUNARELLI-VANDINI (1979), CURTIS (1972, 1977), DALE *et al.* (1989), DANIELSSEN (1859), DAY (1961, 1967), DAY *et al.* (1971), DEWARUMEZ (pers. comm.), DIAPOULIS & BOGDANOS (1983), DUMITRESCO (1960), EAGLE (1973), EAGLE & HARDIMAN (1976), EHLERS (1875), ELIASON (1962), FAUVEL (1909, 1911, 1936, 1937), FAUVEL & RULLIER (1959a,b), FRANKENBERG & LEIPER (1977), GAGE (1972), GAMBI & GANGRANDE (1986), GEORGE (1974), GIANGRANDE & GAMBI (1986), GILLET (1985, 1988), GLÉMAREC (1969), GUELORGET & MICHEL (1979), GUILLAUMONT & HAMON (1983), HAMOND (1966), HARTMAN (1944), HARTMANN-SCHRÖDER (1971, 1974b), HASSAM (1991), HOLTHE (1977b), IBANEZ AGUIRRE & SOLIS WEISS (1986), INTES & LE LOEUFF (1977), JELDES & LEFEVERE (1959), JOHNSON (1901), KINBERG (1867), KIRKEGAARD (1959, 1969, 1978, 1983), LABORDA (1987), LAUBIER (1962), LAVERDE-CASTILLO & GOMEZ (1987), LOPEZ-JAMAR (1981), LOPEZ-JAMAR *et al.* (1986), LUNA (1967), McCALL (1977), McINTOSH (1879, 1915), McINTYRE (1958), McNULTY & LOPEZ (1969), MALMGREN (1867), MARINOV (1977), MASSÉ (1971), MICHAELSEN(1897, 1898), MILLIGAN (1984), NICOLAIDOU *et al.* (1988), NICOLAIDOU & PAPADOPOULOU (1989), NILSEN & HOLTHE (1985), NONATO & LUNA (1970), ORENSANZ & GIANUCA (1974), PEER *et al.* (1980), PROBERT (1981), QUINTINO & GENTIL (1987), REES (1983), REES *et al.* (1976), RIOJA (1917), RULLIER (1963, 1965a), RULLIER & AMOUREUX (1979), SANZ (1986), SHIN *et al.* (1982), STEIMLE (1982), TORRES-GAVILA *et al.* (1990), TREADWELL (1948), TUNBERG (1982), VOVELLE (1963), WACASEY *et al.* (1979), WESENBERG-LUND (1950a, b, 1951, 1953), ZGHAL & BEN AMOR, (1980), ZUNARELLI-VANDINI & COGNETTI-VARRIALE (1981).

Source : MNHN, Paris

In the eastern part of the Pacific Ocean (Fig. 3), it is recorded from Alaska to south California and along the Peruvian and Chilian coasts where it was named *O. fusiformis* or *O. collaris*. In the western part, it is reported from the Bering Sea to Tasmania and New Zealand. It has not been reported from the mid central ocean islands. In the Indian Ocean (Fig. 3), it is present in Bengal Gulf, Arabic Gulf, Mozambic Channel and along Madagascar coasts. It is unknown from the Arabic peninsula to the Mozambique coasts.

In summary, *O. fusiformis* is present along most of the coasts of the Atlantic and Pacific Oceans, it appears less extended in the Indian Ocean and absent in the Antarctic Ocean. Several authors reported *O. fusiformis* as present in this southern Ocean, but the single reference (HARTMAN, 1966) is doubtful because the fragments of tubes were named as ? *Owenia sp.* (Table 2). Therefore, the species occurs in tropical, temperate and arctic areas.

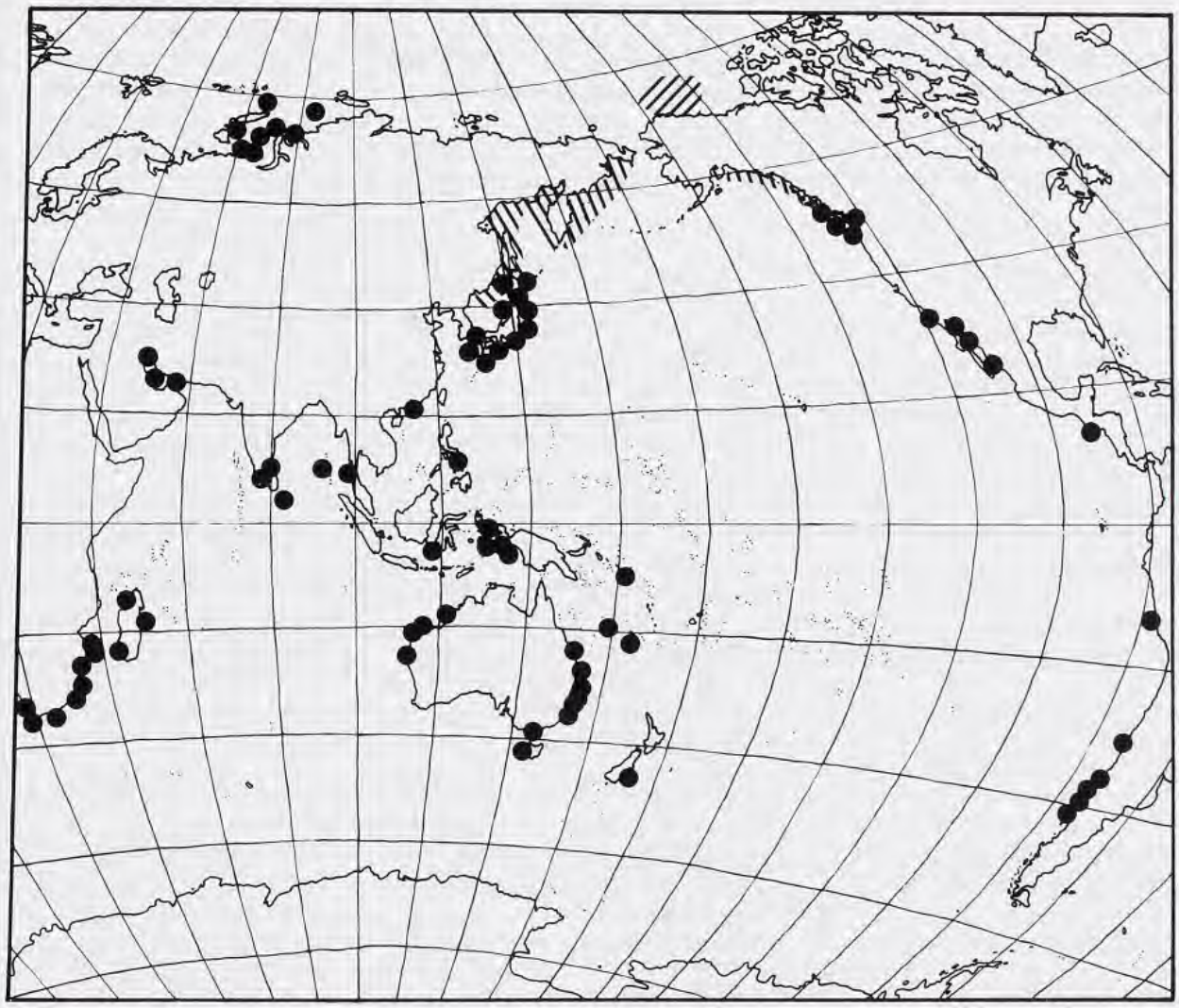


FIG. 3. — The indo-pacific distribution of *O. fusiformis*. From BERKELEY & BERKELEY (1952), BILYARD & CAREY (1979), CAULLERY (1944), CHARDY *et al.* (1987), CLAVIER & GARRIGUE (1990), DAY (1961, 1967), DAY & HUTCHINGS (1979), EHLERS (1901), FAGER (1964), FAUVEL (1911, 1919, 1921, 1932), FOURNIER & LEVINGS (1982), GIBBS (1971), GRUBE (1878), HARTMANN-SCHRÖDER & HARTMANN (1965), HARTMANN-SCHRÖDER (1979, 1980, 1981, 1989, 1990), HASWELL (1883), HOBSON & BANSE (1981), HUTCHINGS (1973), HUTCHINGS & RAINER (1979), IMAJIMA (1961, 1963), IMAJIMA & MORITA (1987), LEE (1976), LEVENSTEIN (1960), LIE & KISKER (1970), NAKO (1982), OKUDA (1937), PLANTE (1967), RAINER (1981), ROZBACZYLO (1985), RULLIER (1965b), SARTI MARTINEZ & SOLIS-WEISS (1987), SHIN & THOMPSON (1982), STEPHENSON & CAMPBELL (1977), TAMPI & RANGARAJAN (1964), THEEL (1879), USCHAKOV (1955), WESENBERG-LUND (1949), WILLEY (1902),WIREN (1883).

Source : MNHN, Paris

TABLE 3. — Records of the main populations of *Owenia fusiformis* (maximal density higher than 100 ind. m-2 or average density higher than 50 ind. m-2). Site, depth and type of community are precised (sieving on 1 mm mesh, except 1: 0,280 and 2: 0,5 mm).

| DEPTHS (m) and SITES | | AUTHOR | TYPE OF COMMUNITY | DENSITY (ind.m-2) |
|---|---|---|---|---|
| | N.E. Atlantic | | | |
| 20-150, Scottish Sea lochs | | GAGE (1972) | muddy sand | two stations : 140, 180 |
| 30, Dogger bank, North Sea | | KIRKEGAARD (1978) | *Venus gallina* | mean : 74 |
| 30, German Bight, North Sea | | RACHOR (1978) | *Nucula turgida* | annual cycles: 0-188 |
| 30, German Bight, North Sea | | SALZWEDEL *et al.* (1985) | " | 0-135 |
| 20-40, " " | | HICKEL *et al.* (1989) | *Abra alba* | several stations: 0-203 |
| 15, N.E. England, North Sea | | REES (1983) | *Venus gallina* | 160 |
| 55, Nothumberland, North Sea | | BUCHANAN *et al.* (1978)<br>BUCHANAN & MOORE (1986) | *Amphiura fififormis*<br>" | annual cycle: 50-410<br>mean 74/80: 75 ; 81/85: 63 |
| 10, Liverpool Bay, Irish Sea | | EAGLE (1973) | *Abra alba* | 275 |
| 2-10, " | | REES *et al.* (1976) | " | 111 |
| 40, Lyme Bay, English Channel | | EAGLE & HARDIMAN (1976) | *Abra alba* | 127 |
| 0, Lannion Bay, English Channel | | AMOUREUX (1966) | *Tellina fabula* | > 1,000 |
| 0, Orne estuary, English Channel | | " | *Tellina fabula* | > 1,000 |
| 10, Bay of Seine, English Channel | | MÉNARD *et al.* (1989) | *Abra alba* | annual cycles : Stn A 385-4,660 |
| 35, Antifer, English Channel | | DAUVIN & GILLET (1991) | *Abra alba* | in Feb. 1987 : 9136 |
| 25, Bay of Seine | | DAUVIN (1992) | " | 300,000 (after recruitment)[1] |
| 5, Penly, English Channel | | GUILLAUMONT & HAMON (1983) | *Abra alba* | annual cycle : 15-117 |
| 23, Off Gironde, Biscay Bay | | BACHELET (1981) | *Abra alba* | 159-325 |
| 30, " | | " | " | 147-422 |
| 38, " | | " | " | 125-1,394 |
| 5-40, Off Arcachon, Biscay Bay | | SANZ (1986) | *Venus gallina* | annual cycles : 0-2,147 (mean: 254) |
| | Mediterranean | | | |
| 5, Prado, Marseille | | MASSÉ (1971) | fine sand | mean: Stn1 367, Stn2 177 |
| 6-7, Camargue, Marseille | | " | " | mean: Stn2 82, Stn3 620 (max. 4940) |
| 1, Prevost Laguna, France | | GUELORGET & MICHEL (1979) | *Scrobicularia plana* | annual cycle: 13-570 |
| 7-10, Roussillon coasts | | AMOUROUX (1974) | *Tellina fabula-tenuis* | 72-444 |
| 10, Alger Bay | | BAKALEM *et al.* (1989) | fine sand | > 100 |
| 12, Adriatic | | COGNETTI-VARIALE & ZUNARELLI-VANDINI (1979) | fine sand & silt | 8,892 |
| 10, Amvrakikos, Greece | | NICOLAIDOU & PAPADOPOULOU (1989) | muddy sand | 25-130 |
| | N.W. Atlantic | | | |
| 9, Georgia shelf | | FRANKENBERG & LEIPER (1977) | fine sand | annual cycle: 0-508 |
| 8, " | | " | very fine sand | " : 20-108 |
| 15-20, Long Island Sound | | MCCALL (1977) | silty sand | > 2,000 |
| 3-5, Biscayne Bay, Florida | | MCNULTY & LOPEZ (1969) | sandy mud | 1,926 |
| | Tropical E. Atlantic | | | |
| 5-20, Gold Coast, Guinea | | BUCHANAN (1957) | fine sand | mean: 5,000 (max. 12,000) |
| | N.E. Pacific | | | |
| 36, Washington coasts | | LIE & KISKER (1970) | fine sand & silt | 460-2,300 |
| littoral, Oregon coasts | | EMMETT *et al.* (1987) | fine sand | mean Sept.: 12,352 (max. 50,246)[2] |
| littoral, Oregon coasts | | EMMETT *et al.* (1988) | fine sand | mean Jul.: 61,582 |
| 8-12, La Jolla Bay, Calif. | S. W. Pacific | FAGER (1964) | fine sand & silt | mean: 500-1,000 (max. 15,000)[2] |
| | S.E. Pacific | | | |
| littoral, Blueskin Bay, N.Z.As *O. collaris* | | RAINER (1981) | shell sand | mean: 4,045 (max. 7,500) |
| 15, Peruvian coasts | | TARAZONA *et al.* (1985, 1988) | fine sand | max.: 18,950 |
| 10, Concepcion Bay, Chili | | OYARZUN *et al.* (1987) | very fine sand | about 5,000 |

Source : MNHN, Paris

## POPULATION DISTRIBUTION *OF OWENIA FUSIFORMIS*

Maximal density (> 100 ind. $m^{-2}$) or mean density (> 50 ind. $m^{-2}$) found in the literature are shown in the Table 3. Maximal densities are found in shallow waters (0-40 m) from fine sand to muddy sand in *Venus, Tellina* or *Abra alba* communities (Table 2). On 0.5 mm sieve mesh, the densities reach a maximum of 300,000 juveniles. $m^{-2}$ during July in the Bay of Seine, English Channel (DAUVIN, 1992), and 50,000 ind. $m^{-2}$ during September on the Oregoncoast (EMMET *et al.*, 1987, 1988). Densities about 5,000 ind. $m^{-2}$ are also reported from the French Mediterranean (MASSÉ, 1971), the Gold coast, Guinea, California, Peru, Chili, and New Zealand (Table 2).

The greater densities were found in cold-temperate waters rather than tropical waters. The other quantitative data with lower densities were: N.E. Atlantic, Norway (HOLTHE, 1977a), North Sea (Mc INTYRE, 1958), Spanish coasts (ANADON, 1980; LOPEZ JAMAR, 1981; LOPEZ JAMAR *et al.*, 1986), Morocco (GILLET, 1988); Mediterranean, Roussillon coasts (GUILLE, 1971)), Ionian Sea (VATOVA, 1975), Tyrrhenian Sea (GIANGRANDE & GAMBI, 1986), Yugoslavia (GILLET, 1985/1986); N.W. Atlantic, Mexican coasts (IBANEZ AGUIRRE & SOLIS-WEISS, 1986), North Carolina (DAY *et al.*, 1971); N.E. Pacific, Columbia coast (FOURNIER & LEVINGS, 1982); N.W. Pacific, Bering Sea (LEVENSTEIN, 1960), Japanese Sea (LEE, 1976; NAKAO, 1982); S.W. Pacific, Chesterfield Island (CLAVIER & GARRIGUE, 1990), New Caledonia (CHARDY *et al.*, 1987); Indian, Nosy Bé (PLANTE, 1967). No relationship between densities and latitude were noted, except in boreal and Arctic waters where lower densities were reported.

## DISCUSSION

The presence of nine shaped papillae around the pygidium is the principal character separating *O. lobopygidiata* from *O. fusiformis*. The other taxa described as *O. ottonis* or *O. assimilis*, which are very close to *O. fusiformis*, are considered as synonyms of *O. fusiformis*. Their descriptions were based on some morphological characters: e.g. number of segments, or number of uncini rows for each torus, which varied with the age of the worms (CAULLERY, 1944; THIEBAUT & DAUVIN, 1992), and cannot be considered as significant taxonomic characters. The status of *O. collaris* characterised principally by the presence of a high, thoracic, membranous collar has been always uncertain, sometimes defined as a valid species (HARTMAN, 1969), and sometimes as a subspecies of *O. fusiformis* (HARTMAN, 1955, 1959). In the Gulf of Mexico, MILLIGAN (1984) does not state the identity of collected specimens possessing a collar. Moreover, ANDREWS (1891) described *O. aedificator* having a delicate membranous collar; later HARTMAN (1959) considered this species as a junior synonym of *O. fusiformis*.

Our study demonstrated the presence of a thoracic collar in all examined specimens from all parts of the world. It showed a more or less important thickness, and this sole morphological difference is insufficient to separate: *O. collaris* from *O. fusiformis*. In conclusion, the *Owenia* genus seems composed of two species: *O. fusiformis* and *O. lobopygidiata*. All other taxa described must be considered as synonymous with *O. fusiformis*.

Except in the Antarctic, the distribution of *O. fusiformis* extends world wide from the cold Arctic to tropical waters. It ranges in depth from low-water mark to the bathyal zone at 2,350 m. Dense populations were limited to shallow waters between 0 to 40 m depth from sandy-mud communities. The greatest densities occurred in areas where fluxes of suspended matter were important: e.g. at the mouth of rivers, Bay of Seine (DAUVIN & GILLET, 1991), or in upwelling zones, Oregon coasts (EMMETT *et al.*, 1987, 1988) or Peru and Chili coasts (TARAZONA *et al.*, 1985; OYARZUN *et al.*, 1987). Low salinities limited its distribution, as in the Baltic. Temperature was not a limiting factor; it is recorded from -1 °C in Arctic waters to more than 30 °C in tropical waters. This result is not a general feature for the polychaetes. WELLS (1963) showed that the distribution of the genera *Arenicola* and *Abarenicola* were correlated with temperature, with the 10 °C and 20 °C surface-water isotherms constituting the most effective barriers for species distribution. Nevertheless, a latitudinal cline of the reproductive period is observed from cold to tropical waters. *O. fusiformis* shows an absence of sexual reproduction in Disko Bay where the species is at its northern limit of distribution forming probably a pseudo-population (CURTIS, 1977).

In the English Channel and North Sea, the species shows a spring and summer spawning and recruitment. In the "Golfe du Lion" and Arcachon Bay a winter spawning and recruitment occurred when the sea bottom temperatures were above 12 °C. Recruitment occured throughout the year in Florida (Key Biscayne) where the water temperature ranged between 23 °C and 28 °C (Mc NULTY & LOPEZ, 1969). This showed that *O. fusiformis* adapts its reproductive strategy to a very broad temperature scale.

The rate of endemism described in some regions (HARTMAN, 1955) should become less as soon as the distribution of some of the species is better known (KIRKEGAARD, 1969). The Polychaeta are generally ancient and

Source : MNHN, Paris

seem to be very conservative (HOLTHE, 1978), which should explain the wide geographical distribution of some species (FAUCHALD, 1984). Cosmopolitan distribution is known for several species of Polychaeta. Nevertheless, three cases of cosmopolitism can be defined: 1) true cosmopolitan distribution: the distribution of a species is really world wide as is *O. fusiformis*; 2) the species is distributed world wide but sibling species have been demonstrated: e.g. *Capitella capitata* (GRASSLE & GRASSLE, 1976); or 3) several species have been confused under the same name: e.g. *Terebellides stroemi* which was divided into five species after a morphological study of specimens from several geographical areas (WILLIAMS, 1984) or *Spio filicornis* which was used for several species of *Spio* (DAUVIN, 1989). Finally, the number of cosmopolitan species could be overestimated (BHAUD, 1982). This is due to three principal causes: 1) the absence of adequate identificatory keys for many parts of the world, 2) the frequent identification of polychaetes by benthic ecologists doing identification work strictly from need, and 3) the poor description of many species (FAUCHALD, 1984).

Recent taxonomic studies of Australian material have revealed in many cases that the species previously identified as the cosmopolitan species *Lanice conchilega* (Pallas, 1766) and *Eupolymnia nebulosa* (Montagu, 1818) were in fact new species (HUTCHINGS & GLASBY, 1988). Moreover Australia is known to have a high speciation rate.

No relationship between the type of development and the range of the distribution of a species has been note (BHAUD, 1982, 1984). Larval stages of certain species could play a role in dispersion (BHAUD, 1982). The main explanation for a wide distribution seems to be the specific responses to physico-chemical, especially temperature conditions (BHAUD, 1982; GOLIKOV *et al.*, 1990). Within the entire distributional area of a species there exists a distinct interrelation between the genetically determined requirements of its individuals and the environment. The distributional pattern indicates a certain unity between the species and its environment, and GOLIKOV *et al.* (1990) suggested the term "ecogenocomplex" for this kind of relationship.

From the data set collected in this work, *O. fusiformis* seems to be a true cosmopolitain species. Since its description by DELLE CHIAJE (1841), several authors have described different species of *Owenia* or, suggested the existence of races of *O. fusiformis* (CAULLERY, 1944; THOMASSIN & PICARD, 1972) by some morphological characters such as the presence of a thoracic collar, the number of segments, the shape of uncini, the length of thoracic setae. However, the morphological and physiological characters used seem to be the result of an interindividual variability and do not permit to separation without ambiguity distinct species. Therefore, most of *Owenia* species described since DELLE CHIAJE have later been considered as a junior synonym of *O. fusiformis*. It is clear that now, as in the past, the macroscopic and microscopic observations or comparisons of morphological characters alone are insufficient to distinguish some possible distinct species of *O. fusiformis*.

In the future, it should be necessary to study *Owenia* with biological and molecular points of view to define its status. Studies must be developed on: 1) the variability and adaptations of reproductive strategy in relation to latitude including extreme conditions as the Arctic and tropical seas; 2) enzymatic and mtDNA polymorphism. For example, GRASSLE & GRASSLE (1976) showed that sibling *Capitella* species with slight morphological differences, and close life histories could be distinguished by genetical characters.

## ACKNOWLEDGEMENTS

The authors would like to thank their colleagues for loan of specimens deposited in their collections: Dr K. FAUCHALD and L. WARD, Smithsonian Institution, Washington, Dr M.C. GAMBI, Stazione Zoologica, Naples, L.H. HARRIS, Natural History Museum of Los Angeles County, Dr G. HARTMANN-SCHRÖDER, Zoologisches Museum, Hamburg, and Dr P. HUTCHINGS, Australian Museum, Sydney. We are also grateful to P. GILLET for access to the library of the Catholic University of Angers and Drs M. BHAUD, K. FAUCHALD and D. REISH for their very constructive suggestions on the first draft

## REFERENCES

AMOUREUX, L., 1966. — Etude bionomique et écologique de quelques Annélides Polychètes des sables intertidaux des côtes ouest de la France. *Arch. Zool. Exp. Gén.*, **107** : 1-218.

AMOUREUX, L., 1970. — Annélides Polychètes du Golfe de Tarente. Résultats de nouvelles croisières de l'Albatros (1968-1969). *Ann. Mus. Civ. di Stor. Nat. di Genova*, **78** : 1-20.

Source : MNHN, Paris

AMOUREUX, L., 1971. — Annélides Polychètes capturés au large de la côte d'Arcachon. Inventaire taxonomique. *Bull. Soc. Linn. Bordeaux*, **1** : 147-164.

AMOUREUX, L., 1972. — Annélides Polychètes recueillies sur les pentes du talus continental, au large de la Galice (Espagne). Campagnes 1967 et 1968 de la "Thalassa". *Cah. Biol. mar.*, **13** : 63-89.

AMOUREUX, L., 1973. — Annélides Polychètes recueillies sur les pentes du talus continental au nord de la côte espagnole. Campagne 1970 de la "Thalassa". *Cah. Biol. mar.*, **14** : 429-452.

AMOUREUX, L., 1976. — Annélides Polychètes récoltées par J. Stirn en 1969, sur les côtes marocaines du détroit de Gibraltar. *Cuad. C. Biol.*, **5** : 5-33.

AMOUROUX, M., 1974. — Étude des peuplements infralittoraux de la côte de Roussillon. III. Variations spatiales et saisonnières. *Vie Milieu B*, **24** : 321-354.

ANADON, R., 1980. — Estudio ecologico de la macrofauna del estuario de la Foz (NO de España): I. Comosicion, estructura, variacion estacional y produccion de las comunidades. *Invest. Pesquera*, **44** : 407-444.

ANDREWS, E.A., 1891. — Report upon the Annelida Polychaeta of Beaufort, North Carolina. *P. U. S. Nat. Mus.*, **14** : 277-302.

AUGENER, H., 1928. — Die Polychäeten von Spitzbergen. *Fauna Arctica*, **5** : 647-834.

BACHELET, G., 1981. — *Étude d'impact des travaux de dragages sur le milieu biologique de l'embouchure de la Gironde (avril 1980-octobre 1980)*. Rapport de Contrat A.D.E.R.A.- Port Autonome de Bordeaux, 59 pp.

BAKALEM, A. & ROMANO, J.C., 1978. — Etude de la dynamique des peuplements benthiques de la baie d'Alger. Résultats préliminaires. *In: IV ème Journées Étud. Pollutions*, Antalya, C.I.E.S.M. : 335-341.

BAKALEM, A., BOUKELLA, H. & ROMANO, J.C., 1989. — Microdistribution du macrobenthos des sables fins de la baie d'Alger. *Pelagos*, **7** : 49-59.

BELLAN, G., 1969a. — Contribution à l'étude des Annélides Polychètes de la région de Rovinj (Yougoslavie). *Rad. Jugosl. Akad. zn. umjet.*, **354** : 25-55.

BELLAN, G., 1969b. — Annélides Polychètes recueillies dans l'archipel de Madère au cours de la campagne scientifique du navire océanographique "Jean Charcot" (juillet 1966). *Cah. Biol. mar.*, **10** : 35-57.

BERKELEY, E. & BERKELEY, C., 1952. — Annelida. Polychaeta Sedentaria. *Can. Pac. Fauna*, **9b** : 1-139.

BHAUD, M., 1972. — Quelques données sur le déterminisme écologique de la reproduction des annélides polychètes. *Mar. Biol.*, **17** : 115-136.

BHAUD, M., 1982. — Relations entre stratégies de reproduction et aire de répartition chez les annélides polychètes. *Oceanol. Acta*, **5** : 465-472.

BHAUD, M., 1984. — Biologie, morphologie et systématique des Annélides Polychètes cosmopolites. *Oceanis*, **10** : 707-721.

BIDENKAP, O., 1894. — Systematisk Oversigt over Norges Annulata Polychaeta. *Forh. VidenskSelsk. Krist.*, **10** : 1-142.

BIDENKAP, O., 1907. — Fortegnelse over de i Trondhjemsfjorden hidtil observerede Annulata Polychaeta. *K. norske VidenskSelsk. Skr.*, **10** : 1-48.

BILYARD, G.R. & CAREY Jr, A.C., 1979. — Distribution of Western Beaufort Sea Polychaetous Annelids. *Mar. Biol.*, **54** : 329-339.

BRUCE, J.R., COLMAN, J.S. & JONES, N.S., 1963. — *Marine fauna of the Isle of Man and its surrounding seas*. Mar. Biol. Univ. Liverpool Press, 307 pp.

BUCHANAN, J.B., 1958. — The bottom fauna communities across the continental shelf off Accra, Ghana (Gold Coast). *Proc. Z. Soc. (London)*, **130** : 1-56.

BUCHANAN, J.B., SHEADER, M. & KINGSTON, P.F., 1978. — Sources of variability in the benthic macrofauna off the south Northumberland coast, 1971-1976. *J. mar. biol. Ass. U. K.*, **58** : 191-209.

BUCHANAN, J.B. & MOORE, J.J., 1986. — Long-term studies at a benthic station off the coast of Northumberland. *Hydrobiologia*, **142** : 121-127.

Source : MNHN, Paris

CAPACCIONI-AZZATI R., VILLORA-MORENO, S., GARCIA-CARRASCOSA, A.M. & TORRES-GAVILA, F.J., 1991. — Distributional patterns of Polychaeta in the Alfaques inlet (Ebro river delta; Western Mediterranean): faunistic and coenotic analysis of an estuarine system. *Bull. Mar. Sci.*, **48** : 369-375.

CARRINGTON, B., 1865. — On the chaetopod annelids of the Southport sands. *Proc. Lit. Philos. Soc. Manchester*, **4** : 176-188.

CASTELLI, A., MORRI, C., BIANCHI, C.N. & DAMIANI, V., 1991. — Benthic Polychaetes from the Tuscan Archipelago (Western Mediterranean). *Bull. Mar. Sci.*, **48** : 585-585.

CAULLERY, M., 1944. — Polychètes sédentaires de l'expédition du Siboga. *Siboga Exped. Leiden*, **24** : 1-204.

CAZAUX, C., 1973. — Cycle et distribution des larves de Polychètes; caractères du méroplancton des différents types de masses d'eaux du bassin d'Arcachon. *Bull. Ecol.*, **4** : 257-275.

CHARDY, P., GERARD, P., MARTIN, A., CLAVIER, J., LABOUTE, P. & RICHER DE FORGES, B., 1987. — Etude quantitative du benthos dans le lagon sud-ouest de Nouvelle-Calédonie. Liste taxonomique, densités et biomasses. *Rapp. Sci. Tech., Sci. Mer, Biol. mar., ORSTOM Nouméa*, **44** : 1-81.

CLAPARÈDE, E., 1868. — Annélides Chétopodes du Golfe de Naples. *Mém. Soc. Phys. Hist. Nat.*, Genève, 19 : 313-584.

CLAVIER, J. & GARRIGUE, C., 1990. — Etude quantitative du macrobenthos dans le lagon des îles Chesterfield. Listes taxonomiques, densités et biomasses. *Rapp. Sci. Tech., Sci. Mer, Biol. mar., ORSTOM Nouméa*, **59** : 1-100

COGNETTI-VARRIALE, A.M. & ZUNARELLI-VANDINI, R., 1978. — Distribution des Polychètes sur les fonds infralittoraux du Molise (Adriatique). *Cah. Biol. mar.*, **19** : 37-45.

COGNETTI-VARRIALE, A.M. & ZUNARELLI-VANDINI, R., 1979. — Polychaetes of littoral sandy bottoms along the north Lazio coast. *Boll. Zool.*, **46** : 77-86.

CURTIS, M.A., 1972. — Depth distributions of benthic Polychaetes in Two fjords on Ellesmere Island, N.W.T. *J. Fish. Res. Bd. Canada*, **29** : 1319-1327.

CURTIS, M.A., 1977. — Life cycle and population dynamics of marine benthic Polychaetes from the Disko Bay area of West Greenland. *Ophelia*, **16** : 9-58.

DALE, J.E., AITKEN, A.E., GILBERT, R. & RISK, M.J., 1989. — Macrofauna of Canadian Arctic fjords. *Mar. Geol.*, **85** : 331-358.

DANIELSSEN, D.C., 1859. — Beretning om en zoologisk Reise i Sommeren. *K. norske VidenskSelsk Skr.*, **4** : 1-78.

DAUVIN, J.C., 1989. — Sur la présence de *Spio decoratus* Bobretzky, 1871 en Manche et remarques sur *Spio martinensis* Mesnil, 1896 et *Spio filicornis* (O.F. Müller, 1776). *Cah. Biol. mar.*, **30** : 167-180.

DAUVIN, J.C. & GILLET, P., 1991. — Spatio-temporal variability in population structure of *Owenia fusiformis* Delle Chiaje (Annelida Polychaeta) from the bay of Seine. *J. Exp. Mar. Biol. Ecol.*, **152** : 105-122.

DAUVIN, J.C., 1992. — Cinétique du recrutement et croissance des juvéniles d'*Owenia fusiformis* Delle Chiaje en baie de Seine (Manche orientale). *Oceanol. Acta*, **15** : 187-196.

DAY, J.H., 1961. — The polychaete fauna of South Africa. Part 6. Sedentary species dredged off Cape coasts with a few records from the shore. *J. Linn. Soc. London*, **44** : 463-560.

DAY, J.H., 1967. — A monograph on the Polychaeta of Southern Africa. Part 2. Sedentaria. *Br. Mus. (Nat. Hist.), London*, **656** : 459-878.

DAY, J.D., FIELD, J.G. & MONTGOMERY, M.P., 1971. — The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. *J. Anim. Ecol.*, **40** : 93-125.

DAY, J.H. & HUTCHINGS, P.A., 1979. — Australian and New-Zealand Polychaeta, Archiannelida and Myzostomida. *Rec. Austr. Mus.*, **32** : 80-161.

DELLE CHIAJE, S., 1841. — *Descrizione e notomia degli animali invertebrati della Sicilia cateriore osservati vivi negli anni 1822-1830*. (5 vol., 137 pls). Naples.

DIAPOULIS, A. & BOGDANOS, C., 1983. - Preliminary study of soft substrate macrozoobenthos and marine flora in the Bay of Gera (Lesvos Island, Greece). *Thalassographica*, **6** : 127-139.

DUMITRESCO, H., 1960. — Contribution à la connaissance des Polychètes de la Mer Noire, spécialement des eaux prébosphoriques. *Trav. Mus. Hist. Nat. "Grigore Antipa"*, **2** : 69-85.

Source : MNHN, Paris

EAGLE, R.A., 1973. — Benthic studies in the South East of Liverpool Bay. *Estuar. Coast. Mar. Sci.*, **1** : 285-299.

EAGLE, R.A. & HARDIMAN, P.A., 1976. — Some variations on the relative abundance of species in a benthic community. *In*: B. KEEGAN, P. O'CEIDIGH & P.J.S. BOADEN (eds), *Biology of Benthic organisms, 11 th European Symposium on Marine Biology*. Pergamon Press, Oxford : 197-208.

EHLERS, E., 1875. — Beiträge zur Kenntniss der Vertikalverbreitung der Borstenwürmer im Meere. *Zeitschr. wiss. Zool.*, **25** : 1-102.

EHLERS, E., 1901. — *Die Polychaëten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch. Festschrift zur Feier des Hunderfünfzijährigen Bestehens des königlichen Gesellschaft der Wissenschaften zu Göttingen (Abh. Math.- Phys.)*. Berlin, 232 pp.

ELIASON, A., 1951. — Reports of the Swedish deep-sea expedition 1947-1948. Polychaeta. *Sc. Lead. Exp.*, **2** : 132-150.

ELIASON, A., 1962. — Untersökningar över ôresund XXXXI. Weitere untersuchu ngen über die Polychaeten fauna des öresunds. *Lunds Univ. Arssk. Avd. 2(58)* : 1-98.

EMMETT, R.N., COLEY, T.C., MCCABE, G.T. & MCCONNELL, R.J., 1987. — *Demersal fishes and benthic invertebrates at four interim dredge sites off the Oregon coast*. Coastal Zone and Estuarine Studies, 69 pp.

EMMETT, R.N., COLEY, T.C., MCCABE, G.T. & MCCONNELL, R.J., 1988. — *Demersal fishes and benthic invertebrates off Tillamook, Oregon, in July 1985*. Coastal Zone and Estuarine Studies, 23 pp.

FAGER, E.W., 1964. — Marine sediments: effects of a tube-dwelling polychaete. *Science*, **143** : 356-359.

FAUCHALD, K., 1977. — Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. *Smith. Contr. Zoology*, **221** : 1-81.

FAUCHALD, K., 1984. — Polychaete distribution patterns, or: can animals with Palaeozoic cousins show large-scale geographical patterns? *In*: P. HUTCHINGS (ed), *Proc. First International Polychaete Conference*. Linnean Society of New South Wales : 1-6.

FAUVEL, P., 1909. — Deuxième note préliminaire sur les Polychètes provenant des campagnes de l'Hirondelle et de la Princesse Alice ou déposés au Musée Océanographique de Monaco. *Ann. Inst. Océanogr. Monaco*, **142** : 1-76.

FAUVEL, P., 1911. — *Annélides Polychètes. Campagne Arctique du Duc d'Orléans de 1907*. Brussels, 45 pp.

FAUVEL, P., 1919. — Annélides Polychètes de Madagascar, de Djibouti et du Golfe Persique. *Arch. Zool. Exper.*, **58** : 317-473.

FAUVEL, P., 1921. — Annélides Polychètes de Madagascar du Muséum R. d'Histoire Naturelle, recueillies par M. le Dr. K. Kaudern en 1912. *Arkiv fôr Zoologi utgivet av K Svenska Vetenskaspakamien Band 13*, **24** : 1-32.

FAUVEL, P., 1932. — Annelida Polychaeta of the Indian Museum Calcutta. *Mem. Ind. Museum Calcutta*, **12** : 1-437.

FAUVEL, P., 1936. — Contribution à la faune des annélides polychètes du Maroc. *Mém. Soc. Sci. Nat. Maroc*, **43** : 1-143.

FAUVEL, P., 1937. — Les fonds de pêche près d'Alexandrie. XI.- Annélides Polychètes. *Notes et Mémoires, Direction des Recherches des Pêcheries*, **19** : 1-60.

FAUVEL, P., 1953. — *Annelida Polychaeta. The Fauna of India*. Indian Press, Ltd, Allahabad, 507 pp.

FAUVEL, P., 1959. — Classe des Annélides Polychètes. Distribution géographique. *In*: P.P. GRASSÉ éd., *Traité de Zoologie*, **5** : 163-165.

FAUVEL, P. & RULLIER, F., 1959a. — Contribution à la faune des annélides polychètes du Sénégal et de Mauritanie (Deuxième note). *Bull. IFAN*, **21** : 934-987.

FAUVEL, P. & RULLIER, F., 1959b. — Résultats scientifiques des campagnes de la "Calypso". Golfe de Guinée. *Ann. Inst. Océanogr.*, **37** : 143-205.

FLINT, R.W. & RABALAIS, N.N., 1980. — Polychaete Ecology and niche patterns: Texas continental shelf. *Mar. Ecol. Prog. Ser.*, **3** : 193-202.

FOURNIER, J.A. & LEVINGS, C.D., 1982. — Polychaetes recorded near two pulp mills on the coast of Northern British Columbia: a preliminary taxonomic and ecological account. *Syllogeus series*, **40** : 1-91.

FRANKENBERG, D. & LEIPER, A.S., 1977. — Seasonal cycles in benthic communities of the Georgia continental shelf. *In*: B.C. COULL (ed), *Ecology of marine benthos*, Univ. South Carolina Press : 383-396.

Source : MNHN, Paris

GAGE, J., 1972. — Community structure of the benthos in Scottish sea-lochs. I. Introduction and species diversity. *Mar. Biol.*, **14** : 281-297.

GAMBI, M.C. & GIANGRANDE, A., 1986. — Distribution of soft-bottom Polychaetes in two coastal areas of the Tyrrhenian sea (Italy): structural analysis. *Estuar. Coast. Shelf Sci.*, **23** : 847-862.

GAMBI, M.C., 1989. — Observazioni sur morfologia funzionale e comportamento trofico di *Owenia fusiformis* Delle Chiaje (Polychaeta, Oweniidae) in rapporto ai fattori ambientali. *Oebalia*, **15** : 145-155.

GENTIL, F. DAUVIN, J.C. & MÉNARD, F. 1990. — Reproductive biology of the Polychaete *Owenia fusiformis* Delle Chiaje in the bay of Seine (eastern English Channel). *J. Exp. Mar. Biol. Ecol.*, **142** : 3-23.

GEORGE, J.D., 1974. — The marine fauna of Lundy Polychaeta (Marine Bristleworms). *Rep. Lundy Fld Soc.*, **25** : 33-48.

GIANGRANDE, A. & GAMBI, M.C., 1986. — Polychètes d'une pelouse à *Cymodoce nodosa* (Ucria) Aschers du golfe de Salerno (Mer Tyrrhénienne). *Vie Milieu*, **36** : 185-190.

GIBBS, P.E., 1971. — The polychaete fauna of the Salomon Islands. *Bull. Brit. Mus. Zool.*, **21** : 101-211.

GILLET, P., 1985. — Annélides Polychètes des fonds meubles du canal de Lim près de Rovinj (Yougoslavie). *Thalas. Jugosl.*, **21/22** : 127-138.

GILLET, P., 1988. — Structure des peuplements intertidaux d'Annélides Polychètes de l'estuaire du Bou Regreg (Maroc). *Bull. Ecol.*, 19 : 33-42.

GLÉMAREC, M., 1969. — *Les peuplements benthiques du plateau continental Nord-Gascogne*. Thèse Doct. Etat, Univ. de Paris, 167 pp.

GOLIKOV, A.N., DOLGOLENKO, M.A., MAXIMOVICH, N.V. & SCARLATO, O.A., 1990. — Theoretical approaches to marine biogeography. *Mar. Ecol. Prog. Ser.*, **63** : 289-301.

GRASSLE, J.P. & GRASSLE, J.F., 1976. — Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science*, **192** : 567-569.

GRAVIER, C., 1906. — Sur l'*Owenia fusiformis* Delle Chiaje et sa distribution géographique. *Bull. Mus. Natn. Hist. Nat. Paris*, **5** : 294-296.

GRUBE, E., 1846. — Beschreibung neuer oder wenig bekannter Anneliden. *Canephorus, Ammochares, Dasymallus, Scalis*-Arten. *Arch. Naturgesch. Berlin*, **12** : 161-171.

GRUBE, E., 1878. — Annulata Semperiana. Beiträge zur Kenntniss der Anneliden-fauna der Philippinen nach den vor Herrn Prof. Semper mitgebrachten Sammlungen. *Acad. Sci. St. Petersburg*, **25** : 1-300.

GUELORGET, O. & MICHEL, P., 1979. — Les peuplements benthiques d'un étang littoral languedocien, l'étang du Prévost (Hérault). 2.- Etude quantitative de la macrofaune des sables. *Tethys*, **9** : 65-77.

GUILLAUMONT, B. & HAMON, D., 1983. — Chapitre IX. Zoobenthos sublittoral. *In*: *Etude écologique de Projet. Site de Penly, 2 ° cycle. Rapport Général*. Centre National pour l'Exploitation des Océans et Electricité de France : 1-47.

HAMOND, R., 1966. — The Polychaeta of the coast of Norfolk. *Cah. Biol. mar.*, **7** : 383-436.

HANSEN, G.A., 1882. — Recherches sur les Annélides recueillies par Mr le Professeur E. van Beneden pendant son voyage au Brésil et à la Plata. *Mém. Cour. Ac. Belg.*, **44** : 1-29.

HARTMAN, O., 1944a. — New England Annelida. Part 2, including the unpublished plates by Verrill with reconstructed captions. *Bull. Amer. Mus. Nat. Hist. New-York*, **82** : 327-343.

HARTMAN, O., 1944b. — Polychaetous Annelids. *Allan Hancock Atlantic Exped.*, **3** : 1-33.

HARTMAN, O., 1955. — Endemism in the north Pacific Ocean, with emphasis on the distribution of marine annelids, and descriptions of new or little known forms. *In*: *Essays in Norb. Sci. in Honor of Capt. Allan Hancock*, Los Angeles: 39-60.

HARTMAN, O., 1959. — Catalogue of the Polychaetous Annelids of the world. *Allan Hancock Foundation, Occasional Paper*, **23** : 1-628.

HARTMAN, O., 1963. — Submarine canyons of Southern California. Part III. Systematics: Polychaetes. *Allan Hancock Pacific Exp.*, **27** : 1-93.

HARTMAN, O., 1965. — Deep-water benthic Polychaetous Annelids off New-England to Bermuda and other North Atlantic areas. *Allan Hancock Found. Publ. Occas. Paper*, **28** : 1-378.

Source : MNHN, Paris

HARTMAN, O., 1966. — Polychaeta Myzostomidae and Sedentaria of Antarctica. *Antarct. Res. Ser.*, **7** : 1-158.

HARTMAN, O., 1969. — *Atlas of Sedentariate Polychaetous Annelids from California*. Allan Hancock Foundation, Los Angeles, 812 pp.

HARTMANN-SCHRÖDER, G., 1959. — Zur Okologie der Polychaeten des Mangrove-Estero-Gebietes von El Salvador. *Beitr. Neotrop. Fauna*, **1** : 69-183.

HARTMANN-SCHRÖDER, G., 1971. — Annelida, Borstenwürmer, Polychaeta. *Tierwelt Dtl.*, **58** : 1-594.

HARTMANN-SCHRÖDER, G., 1974a. — Polychaeten von Expeditionen der "Anton Dohrn" in Nordsee und Skagerrak. *Veröff. Inst. Meeresforsch. Bremerh.*, **14** : 169-274.

HARTMANN-SCHRÖDER,, G., 1974b. — Zur Kenntnis des Eulitorals der afrikanischen Westküste zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostküste von Südafrika und Mocambique unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitt. Hamb. Zool. Mus. Inst.*, **69** : 95-228.

HARTMANN-SCHRÖDER,G. & HARTMANN, G., 1965. — Zur Kenntnis des sublitorals der chilensis Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitt. Hamb. Zool. Mus. Inst.*, **62** : 1-384.

HARTMANN-SCHRÖDER, G., 1979. — *In* : G. HARTMANN-SCHRÖDER, G. & G. HARTMANN, 1979. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden (Teil 2 und 3). Die Polychaeten der trophischen Nordwestküste (zwischen Derby im Norden und Pt. Hedland im Süden). *Mitt. Hamb. Zool. Mus. Inst.*, **76** : 77-218.

HARTMANN-SCHRÖDER, G., 1980. — *In* : HARTMANN-SCHRÖDER & G. HARTMANN, 1980. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden (Teil 4 und 5). Die Polychaeten der trophischen Nordwestküste (zwischen Port Samson im Norden und Exmouth im Süden). *Mitt. Hamb. Zool. Mus. Inst.*, **77** : 41-110.

HARTMANN-SCHRÖDER, G., 1981. — *In* : G. HARTMANN-SCHRÖDER & G. HARTMANN, 1981. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. (Teil 6 und 7). Die Polychaeten der tropish-subtrophischen Westküste (zwischen Exmouth im Norden und Cervantes im Süden). *Mitt. Hamb. Zool. Mus. Inst.*, **78** : 19-96.

HARTMANN-SCHRÖDER, G., 1986. — Die Polychaeten der 56 Reise der "Meteor" zur den South Shetland-Inseln (Antarktis). *Mitt. Hamb. Zool. Mus. Inst.*, **83** : 71-100.

HARTMANN-SCHRÖDER, G., 1989. — *In* : G. HARTMANN-SCHRÖDER & G. HARTMANN, 1989. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden (Teil 14). Die Polychaeten der antiborealen und subtropisch-trophischen Küste Süste Südost-Australiens zwischen Lakes Entrance (Victoria) im Süden und Maclean (New South Wales) im Norden. *Mitt. Hamb. Zool. Mus. Inst.*, **86** : 11-63.

HARTMANN-SCHRÖDER,, G., 1990. — *In*: G. HARTMANN-SCHRÖDER & G. HARTMANN, 1990. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden (Teil 15). Die Polychaeten der subtropisch-trophischen und trophischen Ostküste Australiens zwischen Lake Macquarie (New South Wales) im Süden und Gladstone (Queensland) im Norden. *Mitt. Hamb. Zool. Mus. Inst.*, **87** : 41-87.

HASSAM, N., 1991. — *Contribution à l'étude des peuplements macrobenthiques de la baie de Bou-Ismaïl: secteur est*. Mémoire de Magister, Institut des Sciences de la Mer et de l'Aménagement du Littoral, Alger, 146 pp.

HASWELL, W.A., 1883. — On some new Australian tubicolous Annelids. *Proc. Linn. Soc. New South Wales*, **7** : 633-638.

HICKEL, W., BAUERFEIND, E., NIERMAN, U. & WESTERNHAGEN, H.V., 1989. — Oxygen deficiency in the south-eastern North Sea: Sources and biological effects. *Ber. Biol. Anst. Helgoland*, **4** : 1-148.

HOBSON, K.D. & BANSE, K., 1981. — Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Can. Bull. Fish. Aquat. Sci.*, **209** : 1-132.

HOLTHE, T., 1977a. — A quantitative investigation of the level-bottom macrofauna of Trondheimsfjorden, Norway. *Gunneria*, **28** : 1-20.

HOLTHE, T., 1977b. — The polychaetous annelids of Trondheimsfjorden. *Gunneria*, **29** : 1-64.

HOLTHE, T., 1978. — The zoogeography of the Terebellomorpha (Polychaeta) of the northern european waters. *Sarsia*, **63** : 191-198.

HUTCHINGS, P., 1973. — Polychaeta of Wallis Lake, New South Wales. *Proc. Linn. Soc. New South Wales*, **98** : 175-195.

Source : MNHN, Paris

HUTCHINGS, P. & RAINER, S., 1979. — The polychaete fauna of Careel Bay, Pittwater, New South Wales, Australia. *J. Nat. Hist.*, **13** : 745-796.

HUTCHINGS, P. & GLASBY, C., 1988. — The Amphitritinae (Polychaeta : Terebellidae). *Rec. Austr. Mus.*, **40** : 1-60.

IBANEZ AGUIRRE, A.L. & SOLIS WEISS, V., 1986. — Anélidos poliquetos de las praders de *Thalassia testudinum* del Noroeste de la Laguna de Términos, Campeche, México. *Rev. Biol. Trop.*, **34** : 35-47.

IMAJIMA, M., 1961. — Polychaetous Annelids collected off the West Coast of Kamchatka. I. Notes on species in the collections 1957-58. *Publi. Seto Mar. Biol. Lab.*, **11** : 82-102.

IMAJIMA, M., 1963. — Polychaetous Annelids collected off the West Coast of Kamchatka. II. Notes on species found in the collections 1959. *Publi. Seto Mar. Biol. Lab.*, **11** : 345-370.

IMAJIMA, M. & MORITA, Y., 1987. — Oweniidae (Annelida, Polychaeta) from Japan. *Bull. Natn. Sci. Mus. Tokyo*, **13** : 85-102.

INTES, A. & LE LOEUFF, P., 1977. — Les Annélides Polychètes de Côte d'Ivoire. II. Polychètes sédentaires, compte-rendu systématique. *Cah. O.R.S.T.O.M., Sér. Océanogr.*, **13** : 215-249.

JELDES, F. & LEFEVERE, S., 1959. — Expédition océanographique belge dans les eaux côtières africaines de l'Atlantique Sud. Annélides Polychètes non pélagiques. Seconde note. Polychètes sédentaires. *Inst. Roy. Sci. Nat. Belg.*, **4** : 1-40.

JOHNSON, H.P., 1901. — The Polychaeta of the Puget Sound region. *Proc. Soc. Nat. Hist. Boston*, **1** : 153-190.

KINBERG, J.G.H., 1867. — Annulata nova. *Förh. Oefv. Vet. Akad. Stockholm*, **23** : 337-357.

KIRKEGAARD, J.B., 1956. — Benthic Polychaeta from depths exceding 6000 meters. *Galathea Rep.*, **2** : 63-78.

KIRKEGAARD, J.B., 1959. — The Polychaeta of West Africa. *Atlant. Rept.*, **5** : 7-117

KIRKEGAARD, J.B., 1969. — A quantitative investigation of the central North Sea polychaeta. *Spolia*, **29** : 8-285.

KIRKEGAARD, J.B., 1978. — Production by Polychaetes on the Dogger Bank in the North Sea. *Medd. Danmarks Fisk. og Havunder.*, **7** : 497-509.

KIRKEGAARD, J.B., 1980. — Abyssal benthic Polychaetes from the Northeast Atlantic Ocean, southwest of the British Isles. *Steenstrupia*, **6** : 81-98.

KIRKEGAARD, J.B., 1983. — Bathyal benthic Polychaetes from the N.E. Atlantic Ocean, S.W. of the British Isles. *J. mar. biol. Ass. U.K.*, **63** : 593-608.

KNIGHT-JONES, P., KNIGHT-JONES, E.W. & BUZHINSKAYA, G., 1991. — Distribution and interrelationships of northern spirorbid genera. *Bull. Mar. Sci.*, **48** : 189-197.

LABORDA, A.J., 1987. — Autoecologia de la macrofauna de la playa de Covas : II. Poliquetos sedentarios. *Bol. Inst. Esp. Oceanogr.*, **4** : 47-60.

LARSONNEUR, C., BOUYSSE, P. & AUFFRET, J.P., 1982. — The superficial sediments of the English Channel and its Western approaches. *Sedimentology*, **29** : 851-864.

LAVERDE-CASTILLO, J.J.A. & RODRIGUEZ GOMEZ, H., 1987. — Lista de los poliquetos registrados para el caribe Colombiano, incluyendo comentarios sobre su zoogeografia. *An. Inst. Inv. Mar.*, **17** : 95-112.

LEE, J.H., 1976. — A study on the benthic fauna along the Busan coast, Korea. *Publ. Inst. Mar. Sci. Nat. Fish. Univ. Busan*, **9** : 49-70.

LEVENSTEIN, R.J., 1960. — The quantitative distribution of the Polychaeta in the north western Bering Sea [in russian]. *Trud. Inst. Okeanol.*, **34** : 104-122.

LEVENSTEIN, R.J., 1961. — Polychaeta in the deep-sea area of the Bering Sea [in russian]. *Trud. Inst. Okeanol. Moskva*, **46** : 147-178.

LEVINSEN, G.M.R., 1883. — Systematik-geografisk oversight over de nordiske Annulata. *Vidensk. Medd. dansk. naturh. Foren.* 1883, part 2 : 92-348.

LIE, U. & KISKER, D.S., 1970. — Species composition and structure of benthic infauna communities off the Coast of Washington. *J. Fish. Res. Bd Canada*, **27** : 2273-2285.

Source : MNHN, Paris

LOPEZ-JAMAR, E., 1981. — Spatial distribution of the infaunal benthic communities of the Ria de Muros. North-West Spain. *Mar. Biol.*, **63** : 29-37.

LOPEZ-JAMAR, E., GONZALEZ, G. & MEJUTO, J., 1986. — Temporal changes of community structure and biomass in two subtidal macroinfaunal assemblages in La Coruña bay, NW Spain. *Hydrobiologia*, **142** : 137-150.

LUNA, A., 1967. — Shelf off Alagoas and Sergipe (Northeastern Brazil): 4. Polychaetous Annelids (Preliminary Report). *Trab. Oceanogr. Univ. Fed. Pe., Recife*, **9** : 193-222.

McCALL, P.L., 1977. — Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Mar. Res.*, **35** : 221-266.

McINTOSH, W.C., 1879. — On the Annelida obtained during the cruise of H.M.S. Valorous to Davis Strait in 1875. *Trans. Linn. Soc. London*, n. s., **1** : 499-511.

McINTOSH, W.C., 1915. — Notes from the Gatty Marine Laboratory, St Andrews. *Ann. Mag. Nat. Hist. London*, ser. 8, **12** : 153-181.

McINTYRE, A.D., 1958. — The ecology of scottish inshore fishing grounds. *Mar. Res.*, **1** : 3-17.

McNULTY, J.K. & LOPEZ, N.N., 1969. — Year-round production of ripe gametes by benthic polychaetes in Biscayne Bay, Florida. *Bull. Mar. Sci.*, **19** : 945-954.

MALMGREN, A.J., 1867. — Annulata Polychaeta Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae hactenus cognita. *Forh. Oef. K. Vet. Akad. Stockholm*, **24** : 127-235.

MARINOV, T., 1977. — Polychaeta [in bulgarian). *Fauna Bulg.*, **6** : 1-258.

MARION, A.F., 1876. — Sur les Annélides de Marseille. *Rev. Sci. nat. Montpellier*, **4** : 301-312.

MASSÉ, H., 1971. — *Contribution à l'étude quantitative et dynamique de la macrofaune de peuplements des sables fins infralittoraux des côtes de Provence*. Thèse Doct. Etat, Univ. Aix-Marseille, 310 pp.

MÉNARD, F., GENTIL, F. & DAUVIN, J.C., 1989. — Population dynamics and secondary production of *Owenia fusiformis* Delle Chiaje (Polychaeta) from the Bay of Seine (eastern English Channel). *J. Exp. Mar. biol. Ecol.*, **133** : 151-167.

MICHAELSEN, W., 1897. — Die Polychaeten der deutschen Meere einschliesslich der benachbarten und verbindenten Gebiete. *Wiss. Meeresuntersuch (N. F.)*, **2** : 1-216.

MICHAELSEN,, W., 1898. — Grönlandische Anneliden. *Bibl. Zool. Stuttgart*, **20** : 120-132.

MILLIGAN, M.R., 1984. — Chapter 46. Owenidae. In: J.M. UEBELACKER & P.G. JOHNSON (eds), *Taxonomic guide to the Polychaetes of the northern Gulf of Mexico*. Volume VI. Bary A. VITTOR and associates, Inc., Mobile, Alabama : 1-12.

NAKAO, S., 1982. — Community structures of the macro-benthos in the shallow waters in northern Japan. *Mem. Fac. Fish. Hokkaido Univ.*, **28** : 225-304.

NICOLAIDOU, A., BOURGOUTZANI, F., ZENETOS, A., GUELORGET, O. & PERTHUISOT, J.P., 1988. — Distribution of Molluscs and Polychaetes in Coastal Lagoons in Greece. *Estuar. Coast. Shelf Sci.*, **36** : 337-350.

NICOLAIDOU, A. & PAPADOPOULOU, K.N., 1989. — Factors affecting the distribution and diversity of Polychaetes in Amvrakikos bay, Greece. *P.S.Z.N.I. Mar. Ecol.*, **10** : 193-204.

NILSEN, R. & HOLTHE, T., 1985. — Arctic and Scandinavian Oweniidae (Polychaeta) with a description of *Myriochele fragilis* sp. n., and comments on the phylogeny of the family. *Sarsia*, **70** : 17-32.

NONATO, E.F. & LUNA, J.A.C., 1970. — Anelideos poliquetos do nordeste do Brasil. 1. Poliquetos bentonices da Costa de Alagoas e Sergipe. *Bol. Inst. Oceanogr. Sao Paulo*, **19** : 57-130.

OKUDA, S., 1937. — Spioniform polychaetes from Japan. *J. Fac. Sc. Hokkaido Imp. Univ.*, **5** : 217-254.

ORENSANZ, J.M. & GIANUCA, N.M., 1974. — Contribuiçao ao conhecimento dos Anelideos Poliquetas do Rio Grande do Sul, Brasil. I. Lista sistematica preliminar e descriçao de três novas espécies. *Comun. Mus. Ci. PUCRGS, P. Alerge*, **4** : 1-37.

OYARZUN, C., CARRASCO, F.D. & GALLARDO, V.A., 1987. — Some characteristics of macrobenthic fauna from the organic-enriched sediments at Talcahuano, Chile. *Cah. Biol. mar.*, **28** : 429-446.

Source : MNHN, Paris

PEER, D., WILDISH, D.J., WILSON, A.J., HINES, J. & DADSWELL, M., 1980. — Sublittoral macro-infauna of the lower Bay of Fundy. *Can Tech. Rep. Fish. Aquat. Sci.*, **981** : 1-92.

PLANTE, R., 1967. — Etude quantitative du benthos de Nosy-Bé: note préliminaire. *Cah. O.R.S.T.O.M., sér. Océanogr.*, **5** : 95-108.

PROBERT, P.K., 1981. — Changes in the benthic community of China clay waste deposits in Mevagissey bay following a reduction of discharges. *J. mar. biol. Ass. U.K.*, **61** : 789-804.

QUINTINO, V. & GENTIL, F., 1987. — Etude faunistique et coenotique de la faune annélidienne des lagunes d'Albufeira et Obidos (Portugal). *Cah. Biol. mar.*, **28** : 59-72.

RACHOR, E., 1978. — Changes of macrobenthos in a sublittoral sand area of the German Bight, 1967 to 1975. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, **172** : 418-431.

RAINER, S., 1981. — Soft-bottom benthic communtities in Otago Harbour and Blueskin Bay, New Zealand. *N. Z. Oceanogr. Inst. Mem.*, **80** : 1-38.

REES, H.L., 1983. — Pollution investigations off the north-east coast of England: community structure, growth and production of benthic macrofauna. *Mar. Env. Res.*, **9** : 61-110.

REES, E.I.S., NICOLAIDOU, A. & LASKARIDOU, P., 1976. — The effects of storms on the dynamics of shallow water benthic associations. *In*: B. KEEGAN, P. O'CEIDIGH & P.J.S. BOADEN (eds), *Biology of Benthic organisms*, 11th European Symposium on Marine Biology. Pergamon Press, Oxford : 465-474.

RIOJA, E., 1917. — Datos para el conocimiento de la fauna de Anelidos Poliquetos del Cantabrico. *Trabaj. Mus. Nac. Madrid*, Ser. Zool., **29** : 1-111.

ROZBACZYLO, N., 1985. — Los Anelidos Poliquetos de Chile. *Monografias Biologicas*, 3 : 1-284.

RULLIER, F., 1963. — Les Annélides Polychètes du Bosphore, de la Mer de Marmara et de la Mer Noire, en relation avec celles de la Méditerranée. *Réun. P. V. C.I.E.S.M.M.*, **17** : 161-260.

RULLIER, F., 1965a. — Contribution à la faune des Annélides Polychètes du Dahomey et du Togo. *Cah. ORSTOM Océanogr.*, **3** : 1-57.

RULLIER, F., 1965b. — Contribution à la faune des Annélides Polychètes de l'Australie. *Univ. of Queensland Papers Depart. Zool.*, **2** : 163-201.

RULLIER, F. & AMOUREUX, L., 1968. — Annélides Polychètes du Golfe de Tarente (Italie), résultats des campagnes de l'Albatros (1966-67). *Dagli Ann. Mus. Civ. Stor. Natur. Genova*, **77** : 386- 407.

RULLIER, F. & AMOUREUX, L., 1979. — Annélides Polychètes. Campagne de la Calypso au large des côtes atlantiques de l'Amérique du Sud (1961-1962). *Ann. Inst. Océanogr.*, **55** : 145-206.

SAINT-JOSEPH, A. de, 1898. — Les Annélides des côtes de France (Manche et Océan). *Ann. Sci. Nat.*, **8** : 209-450.

SALZWEDEL, H., RACHOR, E. & GERDES, D., 1985. — Benthic macrofauna communities in the German Bight. *Veröff. Inst. Meeresforsch. Bremerh.*, **20** : 199-267.

SANZ, A., 1986. — Evolution des paramètres de structure des peuplements annélidiens des fonds infralittoraux situés au large du bassin d'Arcachon. *Cah. Biol. mar.*, **27** : 133-152.

SARS, M. 1851. — Beretning om en i Sommeren 1849 foretagen zoologisk Reise i Lofoten og Finmarken. *Nyt Mag. Naturv. Oslo*, **6** : 121-211.

SARTI MARTINEZ, A.L. & SOLIS WEISS, V., 1987. — Estudio prospectivo de la distribucion, abundancia y diversidad de los Anelidos poliquetos de la zona norte del golfo de California. *In*: G. MALAGRINO & H. SANTOYO (eds), *Mem. V Simp. Biol. Mar. Univ. Auton. Baja California Sur* : 53-70.

SHIN, P.K.S., CONNEELY, M.E. & KEEGAN, B.F., 1982. — Littoral and benthic investigations on the west coast of Ireland. XV. The macrobenthic communities of North Bay (Galway Bay). *Proc. Roy. Irish Academy*, **82B** : 133-152.

SHIN, P.K.S. & THOMPSON, G.B., 1982. — Spatial distribution of the infaunal benthos of Hong Kong. *Mar. Ecol. Prog. Ser.*, **10** : 37-47.

STEPHENSON, W. & CAMPBELL, B.M., 1977. — The macrobenthos of Serpentine Creek. *Mem. Qd Mus.*, **18** : 75-93.

STEIMLE, F.W., 1982. — The benthic macroinvertebrates of the Block Island Sound. *Estuar. Coast. Shelf Sci.*, **15** : 1-16.

Source : MNHN, Paris

TAMPI, P.R.S. & RANGARAJAN, K., 1964. — Some Polychaetes Annelids from the Andaman waters. *J. Mar. Biol. Ass. India*, **6** : 98-121.

TARAZONA, J., ARNTZ, W.E., CANAHUIRE, E., AYALA, Z. & ROBLES, A., 1985. — Modificaciones producidas durante "El Niño" en la infauna bentonica de Aaeas someras del ecosistema de Afloramiento Peruano. *In*: W. ARNTZ, A. LANDA & J. TARAZONA (eds), *"El Niño". Su Impacto en la fauna marina*. Bol. Extraordinario Inst. Mar. Peru Callao : 57-63.

TARAZONA, J., SALZWEDEL, H. & ARNTZ, W., 1988. — Oscillations of macrobenthos in shallow waters of the Peruvian central coast induced by El Niño 1982-83. *J. mar. Res.*, **46** : 593-611.

THÉEL, H., 1879. — Les Annélides Polychètes des mers de la Nouvelle-Zemble. *Ofvers. K. VetenskAkad. Förh.*, **16** : 3-75.

THIÉBAUT, E. & DAUVIN, J.C., 1991. — Etude de la fécondité d'*Owenia fusiformis* Delle Chiaje (Annélide Polychète). *J. Rech. Océanogr.*, **16** : 39-41.

THIÉBAUT, E. & DAUVIN, J.C., 1992. — Développement morphologique et croissance des juvéniles d'*Owenia fusiformis* Delle Chiaje (Polychaeta, Oweniidae). *Can. J. Zool.*, **70** : 1701-1711.

THOMASSIN, B.A. & PICARD, C., 1972. — Etude de la microstructure des soies des polychètes Capitellidae et Oweniidae au microscope électronique à balayage : un critère systématique précis. *Mar. Biol.*, **12** : 229-236.

TORRES-GAVILA, F.J., CAPACCIONI-AZZATI, R. & GARCIA-CARRASCOSA, A.M., 1990. — Caracteristicas sedimentarias y fauna de poliquetos de la desembocadura del Rio Segura (Mediterraneo Occidental). *Bentos*, **6** : 81-88.

TREADWELL, A.L., 1948. — Polychaeta. *Canadian Atlantic Fauna, Toronto*, **9** : 1-69.

TUNBERG, B., 1982. — Quantitative distribution of the macrofauna in a shallow, sandy bottom in Raunefjorden, Western Norway. *Sarsia*, **67** : 201-210.

USCHAKOV, P.V., 1955. — Polychaeta of the Far Eastern Seas of the USSR (in russian). *Akad. Nauk SSSR, Keys to the Fauna of the SSSR*, **56** : 1-433. (translated 1965 by Israel Program Scientific Translating, Jerusalem).

VERRILL, A.E., 1885. — Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part V. Annelida, Echinodermata, Hydroida, Tunicata. *Proc. U. S. Nat. Mus.*, **8** : 424-448.

VOVELLE, J., 1963. — Données granulométriques sur le tube des quelques Annélides Polychètes de la plage de Saint Efflam. *Cah. Biol. mar.*, **4** : 315-319.

WACASEY, J.W., ATKINSON, E.G. & GLASSPOOLE, L., 1979. — Zoobenthos data from the upper Frobisher bay, 1967-1973. *Can. Data Rep. Fish. Aquat. Sci.*, **164** : 1-99.

WELLS, G.P., 1963. — Barriers and speciation in lugworms (Arenicolidae, Polychaeta). *Syst. Ass. Publ.*, **5** : 79-98.

WESENBERG-LUND, E., 1949. — Polychaete of the Iranian Gulf. *Danish Sucul. Invest. Iran, Copenhagen*, **4** : 347-400.

WESENBERG-LUND, E., 1950a. — Polychaeta. *Dan. Ingolf Exped.*, **4** : 1-92.

WESENBERG-LUND, E., 1950b. — The Polychaeta of West-Greenland with special reference to the fauna of Nordre Stroemfjord, Krane-, and Bredefjord. *Medd. Groenland.*, **151** : 1-171.

WESENBERG-LUND, E., 1951. — Polychaeta. *Zool. Iceland.*, **2** : 1-182.

WESENBERG-LUND, E., 1953. — The Zoology of East Greenland. Polychaeta. *Medd. Groenland.*, **122** : 1-169.

WILLEY, A., 1905. — Report on the polychaeta collected by Pr. Herdman at Ceylan. *Roy. Soc. Rep. on Pearl Oyster Fisheries, Suppl. Rep.*, **4** : 243-324.

WILLIAMS, S.J., 1984. — The status of *Terebellides stroemi* (Polychaeta: Trichobranchidae) as a cosmopolitan species, based on a worldwide morphological survey, including description of new species. In : P. HUTCHINGS (ed), *Proc. First International Polychaete Conference*. Linnean Society of New South Wales : 118-142.

WILSON, D.P., 1932. — On the mitraria larva of *Owenia fusiformis* delle Chiaje. *Philos. Trans. London, ser.B*, **221** : 231-334.

WIREN, A., 1883. — Chaetopoder fran Sibiriska Ishafvet och Berings Haf insamlade under Vega expeditionen 1878-1879. *In*: A.E. NORDENSKIÖLD (ed), *Vega-exped. Vetensk. iakttagelser*. Stockholm : 383-424.

Source : MNHN, Paris

WOLFF, W.J., 1973. — The estuary as a habitat: an analysis of data on the soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. *Zool. Verhandel. Leiden*, **126** : 1-242.

WOLLEBAEK, A., 1912. — *Nordeuropaeiske Annulata Polychaeta. I. Ammocharidae, Amphictenidae, Ampharetidae, Terebellidae og Serpulidae*. Kommission Hos Jacob Dybwad. Kristiana 144 pp.

ZGHAL, F. & BEN AMOR, Z., 1980. — Annélides Polychètes de Tunisie. *Bull. Off. natn. Pêch., Tunisie*, **4** : 1-11.

ZUNARELLI-VANDINI, R. & COGNETTI-VARRIALE, A.M., 1981. — Effets des décharges polluantes sur une communauté à Polychètes de fonds meubles littoraux. *Cah. Biol. mar.*, **22** : 123-132.

Source : MNHN, Paris

# Light influence on larval emission and vertical swimming in the terebellid worm *Eupolymnia nebulosa* (Montagu, 1818)

*Jean-Claude DUCHÊNE & Christian NOZAIS*

Observatoire Océanologique de Banyuls
Laboratoire Arago
F-66650 Banyuls-sur-mer, France

ABSTRACT

The reproduction of a population of the terebellid worm, *Eupolymnia nebulosa*, was studied at the Arago Marine Laboratory in the western Mediterranean. As many as four spawnings occur from early March to mid June. Eggs are released within jelly masses, counted and collected from a 30 $m^2$ area at various times. Larval outputs from the egg masses were observed. The corresponding swimming activity of the trochophores was measured by mean of an actographic device. The apparatus developed for that purpose allowed fast localisation of sets of up to 400 larvae on a motionless area, or tracking of a single larva by means of computer driven video camera located on translators. The real time video tracking of the swimming larvae allowed precise spatial localisation within gradients. The influence of light was tested on early larvae. Cocoons were analysed in normal and controlled conditions, in order to quantify the number of emerging larvae at different temperatures and growth rates. Larval growth increased with temperature. The larval output from the jelly masses was faster at lower temperatures and high density of larvae within the cocoon. The larval output was closely related to light, increasing the larval swim : most of the larvae were emitted in the plankton during day light. Observations indicated large differences between the four spawnings with implications for recruitment. The first spawning period with lower temperatures, a high phototropy and higher swimming rate of the trochophores resulted in wide larval dissemination. The remaining spawnings, with lower egg density, a higher temperature associated with a faster growth rate, lower swimming activity and longer retention within the cocoon, ensured a good local recruitment.

RÉSUMÉ

**Influence de la lumière sur l'émission et la nage verticale des larves chez le térébellide *Eupolymnia nebulosa* (Montagu 1818)**

Cette étude concerne la reproduction d'une population d'*Eupolymnia nebulosa*, Annélide Terebellidae, située en face du laboratoire Arago, en Méditerranée occidentale. La période de ponte s'étend de mars à juin, avec quatre pics. Les œufs sont pondus dans des cocons muqueux, qui sont recueillis et comptés à diverses périodes sur une surface de référence de 30 $m^2$. L'émission larvaire à partir de ces cocons est étudiée. L'activité de nage des trochophores recueillies est mesurée à l'aide d'un système actographique, développé dans ce but. Ce système permet les enregistrements rapides des positions d'un maximum de 400 larves dans un nuage sur un champ fixe, ou le suivi en temps réel d'un seul individu au moyen de caméras vidéo fixées

DUCHÊNE, J.C. & C. NOZAIS, 1994. — Light influence on larval emission and vertical swimming in the terebellid worm *Eupolymnia nebulosa* (Montagu, 1818). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 405-412. Paris ISBN 2-85653-214-4

Source : MNHN, Paris

sur des translateurs pilotés par un ordinateur. Les enregistrements en temps réel des larves permettent un positionnement précis des larves dans des séries de gradients avec estimation de leur vitesse de nage. L'influence de la lumière a été testée sur les jeunes larves émises à partir des cocons, maintenus en conditions contrôlées, de manière à apprécier le nombre de larves émises dans le temps. La croissance larvaire s'accroît avec la température. La sortie des larves hors des cocons est plus rapide aux basses températures et pour des hautes densités larvaires à l'intérieur des cocons. L'émission larvaire est liée à la lumière, qui augmente l'activité de nage des trochophores et provoque une sortie maximale durant la phase éclairée. Les implications des 4 pontes sur le recrutement sont très différentes : la première période de ponte, lorsque les températures sont basses, la phototropie élevée et le comportement natatoire des larves très actif, favorise une large dissémination. Les pontes suivantes, qui présentent une densité d'œufs plus faible, une température plus élevée associée à un taux de croissance supérieur, une activité de nage plus faible et une rétention accrue au sein des cocons muqueux, favorisent quant à elles un bon recrutement local.

## INTRODUCTION

The reproductive trends of the polychaete *Eupolymnia nebulosa* has been studied for several years in front of the Arago marine laboratory in Banyuls on the western Mediterranean. Personal field observations made by scuba diving revealed that synchronous spawning occurred. On a small submarine cliff, diver observations showed that cocoon production starts at night and lasts until the following week. There were up to four spawning peaks from early March to early June. Records are known for a breeding-ground in front of the laboratory, but concerned only the number of cocoons (GRÉMARE, 1988; BHAUD & GRÉMARE, 1988; DUCHÊNE & NOZAIS, 1992). Larval settlement was analysed in laboratory experiments involving types of sediment and settling in a hydrodynamic flume (BHAUD, 1991; CHIA & BHAUD , 1991). Observations were made in order to estimate the quantity of larvae present over the sediment (DUCHÊNE & NOZAIS, 1992). It appeared that the larval development was highly dependent on external parameters such as temperature (DUCHÊNE, 1982). This modified larval growth and the time when larvae are released from the protective cocoon. Cocoons having different eggs densities were found during the spawning period (DUCHÊNE & NOZAIS, 1992). The first peaks, in March, involve dense cocoons with up to 30,000 eggs. In late May, the mean number of eggs per cocoon had fallen to about 3,500 eggs. The larval density within the cocoon seems to have an influence on the larval release by modifying the structure of the jelly mass. A closer look indicated that larval output from the protective cocoons occured only at certain times of the day. Light appears to be an important synchronising factor for the larval release from the protective cocoon. In order to estimate the influence of the light on larval swimming and behaviour, we developed an actographic device which was able to quantify the displacement of larvae in aquaria with a precision of some microns. The small size of the young *Eupolymnia* larvae led us to adapt the recording system. This involved the use of a small video camera with a magnifying lens mounted on a set of translators allowing large displacement. The field sampled by this camera is very small and compensated by the displacement of the 10 µm precision translators. The only way to automatize this apparatus was to perform a real time analysis on a computer. The camera is then moved by the computer in order to follow the larval displacement.

## MATERIAL AND METHODS

*Eupolymnia nebulosa* larvae are released in the plankton from protective cocoons. The age of every cocoon studied is known from quadrat recordings on the coast in front of the laboratory. The cocoons were gently collected by diver from the rocks from a depth of one meter or less. Each cocoon was isolated in a tank with controlled temperature and light. All the larvae swimming in the tanks were collected and counted every four hours. Individuals were then used for measurement of swimming speed and displacements in controlled light conditions. External recordings of light intensity were used to adapt the controlled light conditions in the tanks.

The age of all larvae used in the measurements was known with a precision of four hours for the March experiments and 12 hours for the other experiments. Larval observations were made within horizontal and vertical tanks. The horizontal tanks were small sized black coated containers with a 6 mm water layer : larvae are attracted by a lateral light source in a non-coated area and when they stop swimming they remain on the bottom of the tank. The vertical tanks were aquaria of various sizes, the most commonly used was 10 x 20 x 40 cm in height.

A set of equipment has been used in this study for locating and counting the young larvae as soon as they are liberated from the mucous cocoon (Fig. 1). Besides the delayed observations realised with the digitizing tablet and the video tape recorder, a real time computer based recording system has been developed in order to achieve a

Source : MNHN, Paris

nearly automatic record of larvae locations within an aquarium. This system is presented on the upper right side of figure 1.

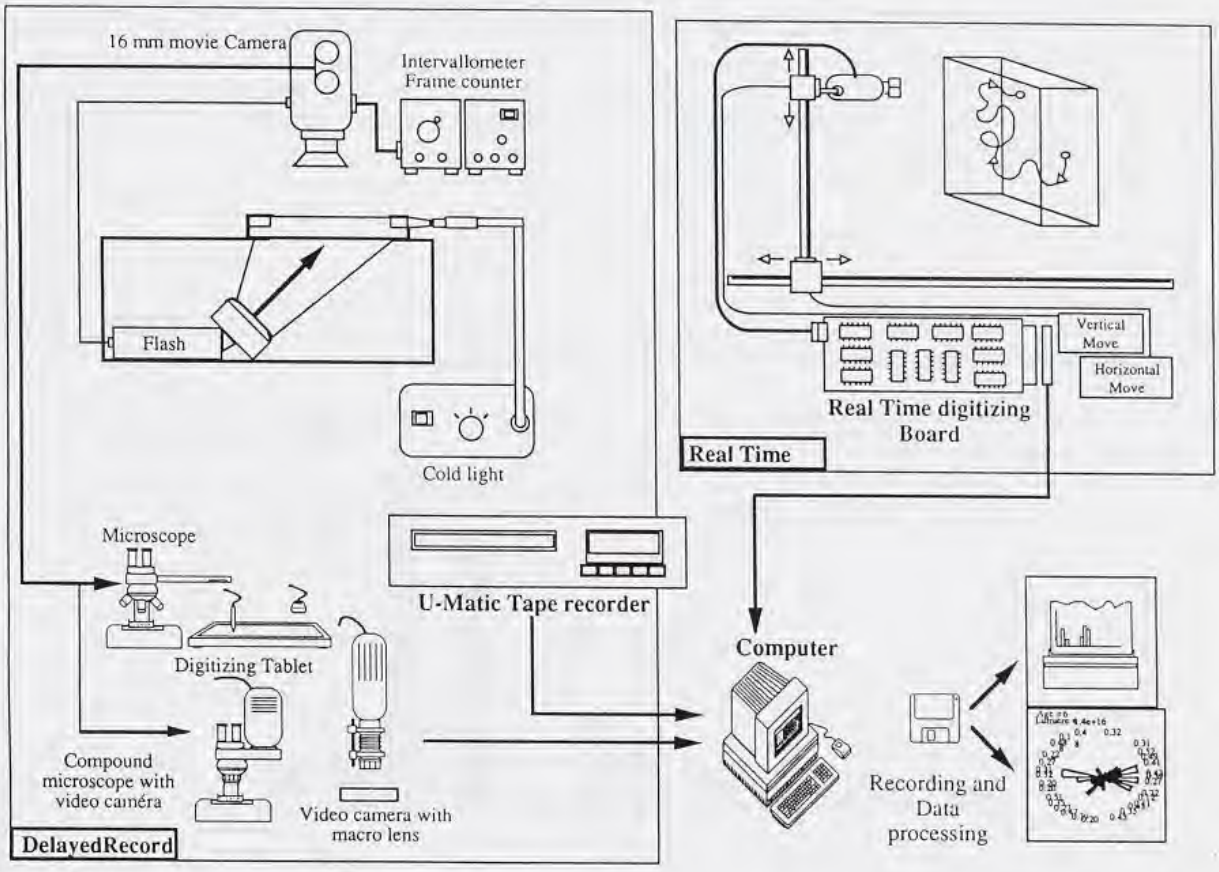



FIG. 1. — Actographic device used for larval displacement measures. Delayed records are made with a video camera connected to U-Matic tape-recorder and with a 16 mm movie camera with intervallometre in order to obtain various recording speeds. The treatment involves a set of digitizers. The real time recordings are made by a computer driven system with video cameras attached on translators allowing size independant measurements (with various optical devices). In the present analysis the size of *Eupolymnia* larvae was between 100 and 220 µm. Motionless measurement of up to 400 larvae or tracking of a single larva over a 1 m distance (length of the longer 12.5 microns precision translator) is possible with the home made software. The real time measurements allow shape extraction and treatment of 4 to 12 frames per second.

A video camera was attached on a X-Y translator driven by step motors. A second camera was mounted at a right angle on the same support to provide depth indications. The step motor translator (CharlyRobot™) allows displacement of video cameras with 12.5 µm steps. Twenty four frames per second are sent to a video digitizer board (MCB™ from Lumiere Technology) connected to a micro-computer (Apple MacIntosh IIcx). A program was developed to insure the video signal analysis. It used MPW-Pascal and MPW-C for the program shell and specific machine language routines (using MPW-Asm) for fast computing related to video acquisition. This resulted in the storage and computation of a pixel matrix followed by the saving of larval location information on text files usable by standard spread sheet programs. The program drives the translators and computes relative displacements. The recording/computing process allowed a mean speed of about 4-12 frames. $s^{-1}$, depending on the type of recording.

Two different modes were tested during larval analysis :

- a "cloud" analysis of a set of up to 400 larvae (generally we used 50 larvae) with recordings of the analysed video field every tenth of a second. In this case the computer system is used like the standard tape recording video

Source : MNHN, Paris

analysis systems with a real time analysis instead of a delayed study of the shapes. We used a motionless camera mode for the study (the barycenter of the larval group may be calculated with associated camera translation). This allowed us to make precise estimations of the light conditions for every place in the video field.

- a single individual tracking, with long displacements (the larger translator allows a maximum displacement of 1,020 mm). When the larva was about to quit a control area, the computer sends indications to the electronic board controlling the camera translators. The shape is then brought back to the centre of the survey zone and its displacement is taken into account.

Irradiances used in the experiments remain within the range observed in the field (maximum of $9 \times 10^{16}$ Q. $cm^{-2}$. $s^{-1}$ at a 20 cm depth). We selected a range corresponding to the transition observed from positive to negative phototaxic response (1 to $1.8 \times 10^{16}$ Q. $cm^{-2}$. $s^{-1}$).

## RESULTS

The larval output from the protective cocoons begins early in March and ends in late May. Observations on the number of larvae swimming out of the protective egg mass indicated a diurnal emission : the maximum number of larvae emerging from the cocoons occurred between 10 AM and 6 PM (Fig. 2).

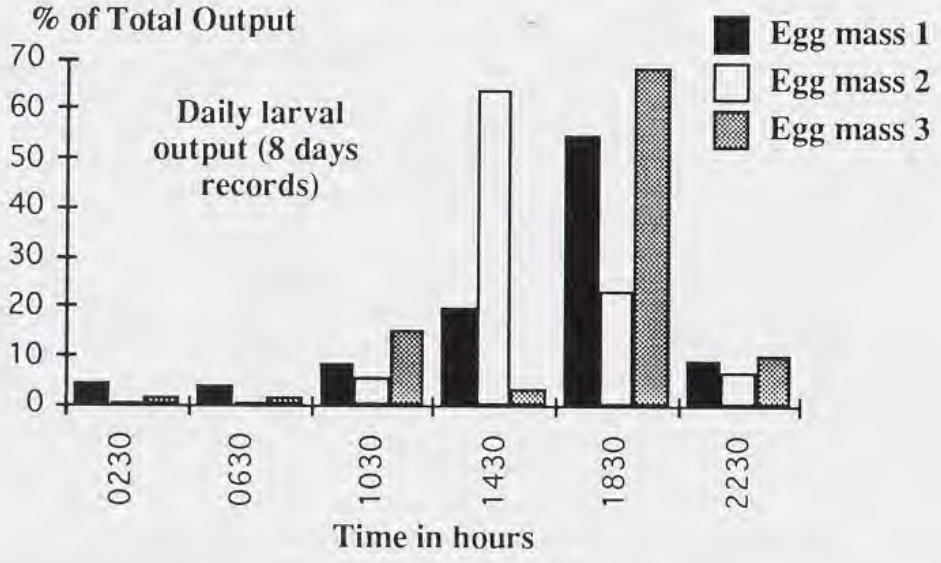



FIG. 2. — Number of larvae swimming out of the protective cocoon at different hours of the day. The cocoons are empty after 8 days. The presented percentages are summed up for every class of time and for 3 different egg masses in March 91. The main larval output occurs between 10h30 and 18h30.

Clear photopositive reaction was measured in the first free swimming stages: all the individuals between three and 10 days were found close to the light source within a few minutes. The swimming speed of the three day old larvae increased with light intensity. The four day old larvae swim actively toward the light source and remain 1.0 mm from the surface. The photopositivity decreased with age: the 10 day old larvae were found in a 5 mm layer below the surface.

The swimming behaviour of *E. nebulosa* larvae consists of short periods of fast swimming towards the light source and long, scattered periods of rest or slow motion. As shown in Table 1, 24 % of the swimming of a three day old larva is directed toward the light with an average speed of 0.982 mm. $s^{-1}$, and 76 % of the displacement are active sinking periods with a slow upward motion compensating passive sinking, resulting in a downward movement with a mean speed of 0.35 mm. $s^{-1}$. This is demonstrated by records of anaesthetized larvae presenting a downward displacement with values ranging from 1.3 to 1.7 mm. $s^{-1}$.

Observations were made to find the illumination corresponding to a general switch from photopositive to negative displacement in a light gradient (Fig. 3). For the observations made in the vertical tanks, the negative displacements consisted in a reduction of the active upward swimming phases, resulting in semi-passive sinking.

Source : MNHN, Paris

In horizontal tanks movements were active in both directions. The illumination level did not change during the

TABLE 1. — Swimming speed of *Eupolymnia nebulosa* larvae of different ages. The range and the mean of the upward and downward speeds of non anaesthetized animals are given, for the variations are important depending on the intensity of the light. The 95 % confidence interval is shown for anaesthetized individuals. Numbers of measures is 4,275 for 3-4 days larvae, 1,023 for 7 days larvae, 502 for anaesthetized 4 days larvae, and 184 for anaesthetized 7 days larvae.

| | % Upward moves | Upward speed (mm. $s^{-1}$) | % Downward moves | Downward speed (mm $s^{-1}$) |
|---|---|---|---|---|
| 3-4 days larvae<br>Mean | 24.21 % | 0.6 - 1.44<br>0.982 | 75.79 % | 0.18 - 0.47<br>0.35 |
| 7+ days larvae<br>Mean | 32.26 % | 0.289 - 1.183<br>0.740 | 67.74 % | 0.27 - 0.80<br>0.56 |
| anaesthetized<br>4 days larvae | | | 100 % | 1.52±0.02 |
| anaesthetized<br>7+ days larvae | | | 100 % | 0.94±0.05 |

resting phase, because of the larval settling on the bottom of the tank. The larvae had to swim actively away from the light source. The scale differences in the net displacements, in figure 3, reflect this major difference: a reduction in swimming in a vertical tank results in sinking (negative speed in the gradient) when the same reduction in the horizontal tank may result in a settling, with a null speed.

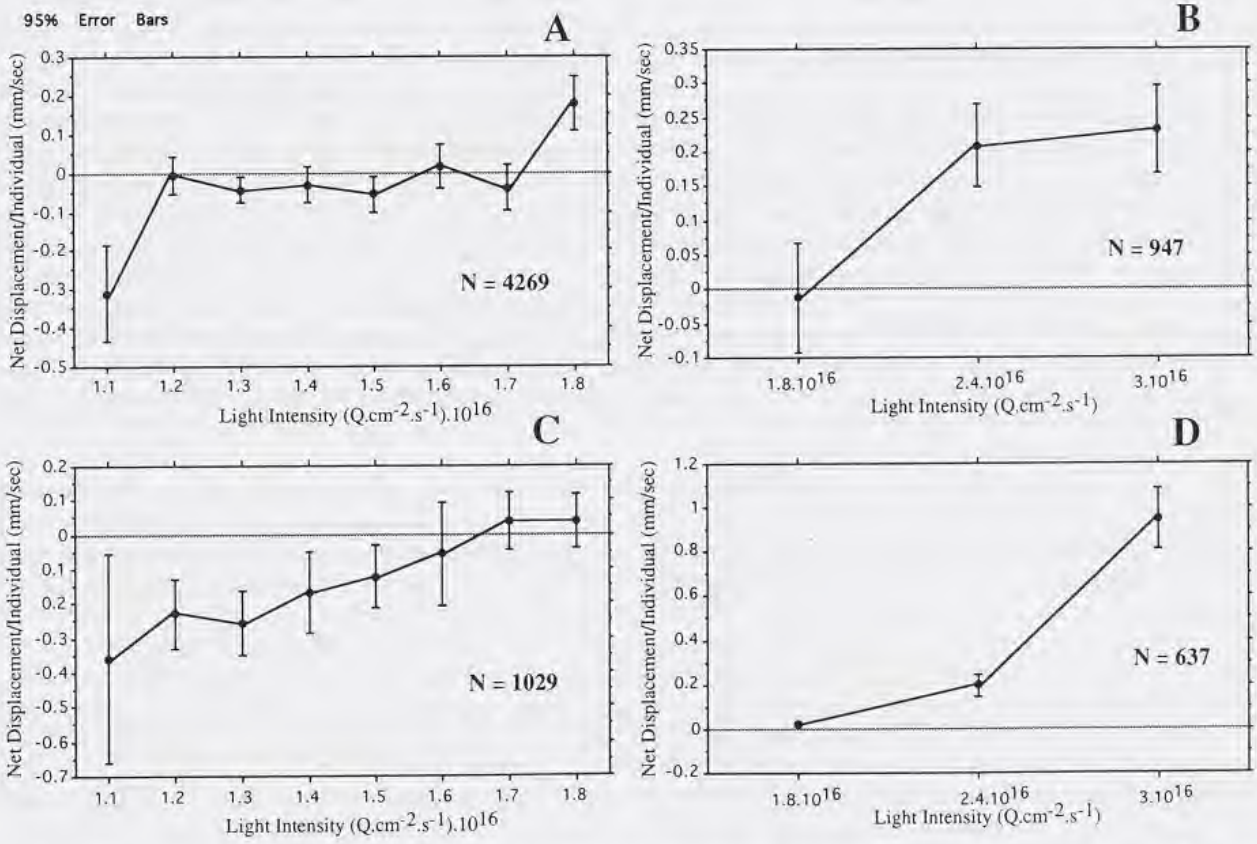



FIG. 3. — Measurements on larval swimming as a function of light intensity in vertical (A and C) and horizontal (B and D) tanks. Net displacements correspond to the mean displacement of a set of several larvae for 2 different ages (A-B: 4 day old larvae; C-D: 7 day old larvae). The grey line corresponds to neutral buoyancy. N represents the number of larvae used for the 95 % confidence interval.

Source : MNHN, Paris

From figure 3 it appears that the switch from positive to negative swimming occurs for light intensities ranging from 1 to 2 x $10^{16}$ Q.cm$^{-2}$. s$^{-1}$. Lower illuminations always correspond to sinking, higher illuminations to upward swimming. The differences between four day and seven day old larvae depended on the position and the pattern of the inversion: older larvae needed a stronger stimulus to increase their swimming rate. The maximum mean speed toward the stimulus, computed by considering only the positive displacements is :

- 1.34± 0,09 mm. s$^{-1}$ for an illumination of 1.6 x $10^{16}$ Q. cm$^{-2}$. s$^{-1}$ for 4 day old larvae;
- 1.17± 0,04 mm. s$^{-1}$ for an illumination of 1.4 x $10^{16}$ Q. cm$^{-2}$. s$^{-1}$ for 7 day old larvae.

The net displacement is not only related to the mean speed of movement toward the light source but also to the swimming/rest ratio. The data in figure 3 suggest that this ratio increased with the intensity of the stimulus and reached higher values for older larvae at higher light intensities. In the vertical tanks the records concerning larvae remaining close to the surface have been eliminated.

## DISCUSSION AND CONCLUSIONS

Studies involving terebellid polychaetes revealed the importance of early protection during the first developmental stages within egg masses. The positive phototropic response of trochophores of *Eupolymnia* in first stages increased the dispersion of larvae by causing them to swim toward the surface. This had been observed with the subantarctic polychaete, *Thelepus extensus* (DUCHÊNE, 1982). In both cases the first free swimming stages emerging from the cocoon were usually strongly sensitive to light. Larvae may change their response toward specific physical parameters during their planktonic life. A late negative phototropy was found in many cases which lead to increased settling on the benthos.

When the larvae were released to the plankton they can remain in a free swimming period for varying lengths depending upon the environmental conditions and the specific abilities of the larvae. These terebellid trochophores have lecithotrophic development and may be present in the plankton as long as 2-3 days, however, the settling trials start shortly after the release from the egg mass. Local modifications may be found: it seems likely that the early *Thelepus extensus* larvae released from the outer parts of the cocoon stay within the plankton for a longer time than the inner larvae (personal observations, in Kerguelen Archipelago). These later ones continue their development within the spherical chambers inside the cocoon and the free swimming stage is then reduced. Larvae are likely to stay for a longer or shorter time in the plankton depending on the positionin the cocoon. *Eupolymnia* larval densities inside the jelly masses appear to modify the emission patterns (DUCHÊNE & NOZAIS, 1992). There is also a possible relationship between physical parameters and vitellogenesis. Differences in the number of eggs per spawn are important. The number of eggs in the cocoons is high during the first spawning period in March when the water temperature is low and the larval growth slow. A high proportion of young stages is emitted to the plankton. At that period only a part of the oocyte production is spawned. The physical size of the mucous cocoon may be involved in this limitation together with the state of oocyte maturation. An active selection of large-sized oocytes is made by the ciliated nephrostome. The smaller oocytes remain within the coelom. Selection is probably achieved by a mechanism which detects the shape of spherical mature oocytes within the coelomic cavity as opposed to immature ones which are flattened.

Numerous attempts to measure animal displacements have been made including real time analysis systems (ROONEY & COBB, 1991; BAKCHINE-HUBER *et al.*, 1992; BOISCLAIR, 1992). The real time device with robotized cameras used in this study allows flexible analysis of larval movements on large surfaces. Planktonic larvae are often swimming rather fast with spiral, undulating direction components, making the precise localisation difficult. The analysis of response to physical stimuli is therefore complex, due to the inherent complexity of the normal larval displacement. A spiral swimming movement may be distorted by a response to positive light influence. The general trend will be a displacement toward the light emission. In that particular case (stimulus easy to localize and to interpret) the correlation is simple and the observer is able to describe the overall larval response. With other stimuli such as salinity, temperature gradients or sediment attraction, identification of the source of the larval displacement is difficult to make and developmental stage must be taken into consideration.

To determine the relationship between hydrodynamics and the movement of larvae, the abilities of some invertebrate larvae to move horizontally or vertically have been investigated by KONSTANTINOVA (1966, 1969), MILEIKOVSKY (1973) and CHIA *et al.* (1984); but swimming direction was not always specified. More recently BUTMAN *et al.* (1988) measured swimming speeds and sinking velocities of two sibling species of *Capitella*. Their swimming speed varied between 2 and 4 mm. s$^{-1}$. Horizontal movements of large amplitude or the transportations of long duration seem to be the characteristic of ciliated larvae endowed with efficient trochae. This is found in the

Source : MNHN, Paris

larvae of Nephtyidae, Spionidae or Chaetopteridae (CAZAUX, 1981). The use of parapodia is found in the nectochaetes of Aphroditidae. Nectosomes of Poecilochaetidae move by snake-like undulating movements (BHAUD & CAZAUX, 1988). Larvae without swimming apparatus or reduced cilia, for example Orbiniidae, Lumbrineridae, do not possess the ability to rise in the water column and are observed rarely in planktonic samples. However, some species such as *Lanice conchilega* with aulophore larvae lack a swimming device and are collected in large numbers in the water column.

Observations on larval motion appear to be of interest when dissemination and settling considerations are analyzed. If large-scale dispersal of planktonic larvae is determined mainly by oceanic circulation (SCHELTEMA, 1971; PALMER, 1988), larval behaviour may influence settling probability at very small spatial scales (CRISP, 1974; ECKMAN, 1983). The larval swimming speed is generally too low in comparison with currents to have an effect on horizontal movements. As pointed out by CHIA *et al.* (1984) larval swimming may however influence the vertical migrations. Vertical distribution is likely to be controlled by vertical motions except when stratification exists (MILEIKOVSKY, 1973). THORSON (1964) proposed vertical movements could be the result of ontogenic changes in photoresponse which appear sometimes during larval life. Those predictions have been confirmed by laboratory observations (MARSDEN, 1984, 1986, 1990), field observations (YOUNG & CHIA, 1982a, b) and correlated data (FORWARD *et al.*, 1984). Many studies show that light strongly influences larval behaviour (FORWARD & COSTLOW, 1974; VIA & FORWARD, 1975).

The larval emission recorded in these experiments shows that the release in the plankton of more than 90% of the larvae occurs during the day and generally during the highest local illumination period. Light intensities at this period recorded close to the water surface level (20 cm depth) were between 2.4 and 9 x $10^{16}$ Q. $cm^{-2}$. $s^{-1}$.

Light intensity necessary to switch from positive to negative motion appears to be located in a rather narrow range for the young *E. nebulosa* studied in this set of experiments (4-7 days old). The response to a light stimulus corresponds to an increase of the swimming speed with a positive/negative heading and to a modification of the larval behaviour (rest/swim ratio or settling tendency/light stimulation constraint). In March, response to light induces upward swimming proportional to the intensity of the stimulus. In this case, the light stimulus seems to increase the dissemination phase (first spawning). Later in the season, when natural light intensity increases, the larvae are emitted in the plankton in lower densities and at a later developmental stage, resulting in a reduced photosensitivity and a reduced swimming phase. The positive displacement of seven day old stages at high illumination levels is still possible, but most these stages are usually found within the jelly masses. In the bay facing the marine laboratory in Banyuls, rotary motion currents allow planktonic larval retention over precise areas. The continuous current speed observations indicate clearly that the larvae are unable to swim against the current flow. On the contrary, the vertical motions observed indicate clearly a possible vertical displacement from the shallow water sediment, where the larvae are emitted to the surface and back. The vertical structure of the water masses shows a clear and rather constant reversal of the current direction depending on the depth (DUCHÊNE, 1994, in prep.). In these conditions a short vertical migration may induce a complete reversal in passive transportation by the currents. The vertical swimming observed in the *Eupolymnia* larvae is sufficient to allow this transition from an out of the bay to an inward motion.

## ACKNOWLEDGEMENTS

This study is a contribution to the French National Program on the Determinism of Recruitment by a grant conceded to the Laboratory.

## REFERENCES

BAKCHINE-HUBER, E., MARION-POLL, F., PHAM-DELEGUE, M.H., MASSON, C., 1992. — Real-time detection and analysis of the exploratory behavior of small animals. *Naturwissenschaften*, **79** : 39-42.

BHAUD M., 1991. — Larval release from the egg mass and settlement of *Eupolymnia nebulosa* (Polychaeta, Terebellidae). *Bull. mar. Sci.*, **48** : 420-431.

BHAUD, M. & C. CAZAUX, 1988. — Description and identification of Polychaete larvae; their implications in current biological problems. *Oceanis*, **13** : 596-753.

BHAUD, M., GRÉMARE A., 1988. — Larval development of the terebellid Polychaete *Eupolymnia nebulosa* (Montagu, 1818) in the Mediterranean Sea. *Zool. Scripta*, **17** : 347-356.

Source : MNHN, Paris

BOISCLAIR, D., 1992. — An evaluation of the stereocinematographic method to estimate fish swimming speed. *Can. J. Fish. Aquat. Sci.*, **49** : 523-531.

BUTMAN, C.A., GRASSLE, J.P., BUSKEY, E.J., 1988. — Horizontal swimming and gravitational sinking of *Capitella capitata* sp.I (Annelida: Polychaeta) larvae: implications for settlement. *Ophelia* , **29** : 43-57.

CAZAUX, C., 1981. — Evolution et adaptation larvaires chez les Polychètes. *Oceanis*, **7** : 43-77.

CHA, J.H., BHAUD, M., 1991. — Etude expérimentale du recrutement benthique en canal hydrodynamique et en milieu calme. *C.R. Acad. Sci.*, **312** Sér.3 : 113-118.

CHIA, F.S., BUCKAND-NICKS, J., YOUNG, C.M., 1984. — Locomotion of marine invertebrate larvae: a review. *Can. J. Zool.*, **62** : 1205-1222.

CRISP, D.J., 1974. — Factors influencing the settlement of marine invertebrate larvae. *In*: P.T. GRANT & A.M. MACKIE (eds), *Chemoreception in marine organisms*, Academic Press, 1974.

DUCHÊNE, J.C., 1982. — *Étude comparée de la biologie d'Annélides Polychètes considérées en différentes zones climatiques*. Thèse de Doctorat d'Etat, ès Sci. Nat., Univ. P. & M. Curie, 1-315 pp.

DUCHÊNE J.C., NOZAIS, CH., 1992. — Etude de l'émission des stades larvaires précoces d'*Eupolymnia nebulosa* (Polychaeta : Terebellidae). *Annales Inst. Océanogr.*, **68** : 15-24.

ECKMAN, J.E., 1983. — Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.*, **28** : 241-257.

FORWARD, R.B., Jr., COSTLOW, J.D., Jr., 1974. — The ontogeny of phototaxis by larvae of the crab *Rhithropanopeus harrisii*. *Mar. Biol.*, **26** : 27-33.

FORWARD, R.B., Jr., CRONIN, T.W., STEARNS, D.E., 1984. — Control of diel vertical migration: Photoresponses of a larval crustacean. *Limnol. Oceanogr.*, **29** : 146-154.

GRÉMARE, A., 1988. — *Aspects quantitatifs de la reproduction chez quelques Annélides Polychètes : Intérêts et perspectives*. Thèse Doctorat d'Etat, Univ. P. & M. Curie, 218 pp.

KONSTANTINOVA, M.I., 1966. — Characteristic movement of pelagic larvae of marine invertebrates. *Dokl. Akad. Nauk. SSSR*, **170** : 726-729.

KONSTANTINOVA, M.I., 1969. — Movement of polychaete larvae. *Dokl. Akad. Nauk. SSSR*, 188 : 942-945.

MARSDEN, J.R., 1984. — Swimming in response to light by larvae of the tropical serpulid *Spirobranchus giganteus*. *Mar. Biol.*, **83** : 13-16.

MARSDEN, J.R., 1986. — Response to light by trochophore larvae of *Spirobranchus giganteus*. *Mar. Biol.*, **93** : 13-16.

MARSDEN, J.R., 1990. — Light responses of the planktotrophic larva of the serpulid polychaete *Spirobranchus polycerus*.. *Mar. Ecol. Prog. Ser.*, **58** : 225-233.

MILEIKOVSKI, S.A., 1973. — Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Mar. Biol.*, **23** : 11-17.

PALMER, M.A., 1988. — Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Mar. Ecol. Prog.Ser.*, **48** : 81-91.

ROONEY, P., COBB, J.S., 1991. — Effects of time of day, water temperature, and water velocity on swimming by postlarvae of the American Lobster, Homarus americanus. *Can. J. Fish. Aquat. Sci.*, **48** : 1944-1950.

SCHELTEMA, R.S., 1971. — Larval dispersal as a means of genetic exchange between geographically separated populations of shoal-water benthic marine gasteropods. *Biol. Bull.*, **140** : 284-322.

THORSON, G., 1964. — Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. *Ophelia*, **1** : 167-208.

VIA, S.E., FORWARD, JR., R.B., 1975. — The ontogeny and spectral sensitivity of polarotaxis in larvae of the crab *Rhinthropanopeus harrisi* (Gould). *Biol. Bull.*, **149** : 251-266.

YOUNG, C.M., CHIA, F-S., 1982a. — Ontogeny of phototaxis during larval development of the sedentary polychaete, *Serpula vermicularis* (L.). *Biol. Bull.*, **162** : 457-468.

YOUNG, C.M., CHIA, F.S., 1982b. — Factors controlling spatial distribution of the sea cucumber *Psolus chitonoides*: settling and post-settling behavior. *Mar. Biol.*, **69** : 195-205.

Source : MNHN, Paris

# Polychaeta of the German Bight from the 1987 cruise of the R/V "Senckenberg"

*Dieter FIEGE** & *M. Nechana BEN-ELIAHU***

*Forschungsinstitut Senckenberg, Sektion Marine Evertebraten II
Senckenberganlage 25 D-6000 Frankfurt/M., Germany
**The Life Sciences Collections, The Hebrew University of Jerusalem
91904 Jerusalem, Israel

## ABSTRACT

The present paper reports on the collections of Polychaeta of the 1987 cruise to the German Bight, "DEB 1987". Fifty-one samples from 25 stations covering a depth range from 14 to 46 m were analyzed. The samples contained about 1,500 polychaetes in 46 genera in 29 families. Altogether, 67 separate taxa were determined, of which 63 were identified to species. As many as 26 species per sample were found. The distribution of species in the samples is discussed.

## RÉSUMÉ

**Polychètes de la grande baie allemande récoltées par le R/V "Senckenberg" au cours de la campagne de 1987**

Dans cette note les résultats des récoltes des polychètes de l'expédition 1987 dans le golfe allemand, "DEB 1987", sont présentés. Cinquante et un échantillons provenant de 25 stations, dont les profondeurs varient entre 14 et 46 m, ont été analysés. Les échantillons contenaient environ 1500 polychètes appartenant à 46 genres de 29 familles. Soixante sept espèces ont été distinguées, dont 63 ont pu être déterminées. On a trouvé jusqu'à 26 espèces par échantillon. La distribution des espèces dans les échantillons est discutée.

## INTRODUCTION

Benthic communities and species distribution in the North Sea have been studied by various authors (STRIPP, 1969; STRIPP & GERLACH, 1969; GLÉMAREC, 1973; McINTYRE, 1978; RACHOR & GERLACH, 1978; ZIEGELMEIER, 1978; SALZWEDEL *et al.*, 1985; BASFORD *et al.*, 1989; FRAUENHEIM *et al.*, 1989; KÜNITZER, 1990). Investigations with special emphasis on the distribution of Polychaeta in the area have been carried out by MICHAELSEN (1897), FRIEDRICH (1938), HARTMANN-SCHRÖDER & STRIPP (1968), and KIRKEGAARD (1969).

FIEGE, D. & M. N. BEN-ELIAHU, 1994. — Polychaeta of the German Bight from the 1987 cruise of the R/V "Senckenberg". *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 413-423. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

The latter reviews the previous collections in the North Sea. Earlier investigations were often limited to particular areas within the North Sea (TÜRKAY, pers. comm.). The fauna of the northern North Sea is still poorly known in regards to both in- and epifaunal benthic invertebrates (BASFORD *et al.* (1989).

The Senckenberg Research Institute began a long-term study of epizoobenthos in the North Sea in 1977 in order to obtain a comprehensive view of the distribution of different taxa and to establish baseline data for monitoring possible changes in the future.

Fifteen annual cruises have been carried out during summers to different areas within the North Sea. More than 200 stations have been sampled to date. The present paper reports on the collections of Polychaeta made during the 1987 expedition to the German Bight "DEB 1987".

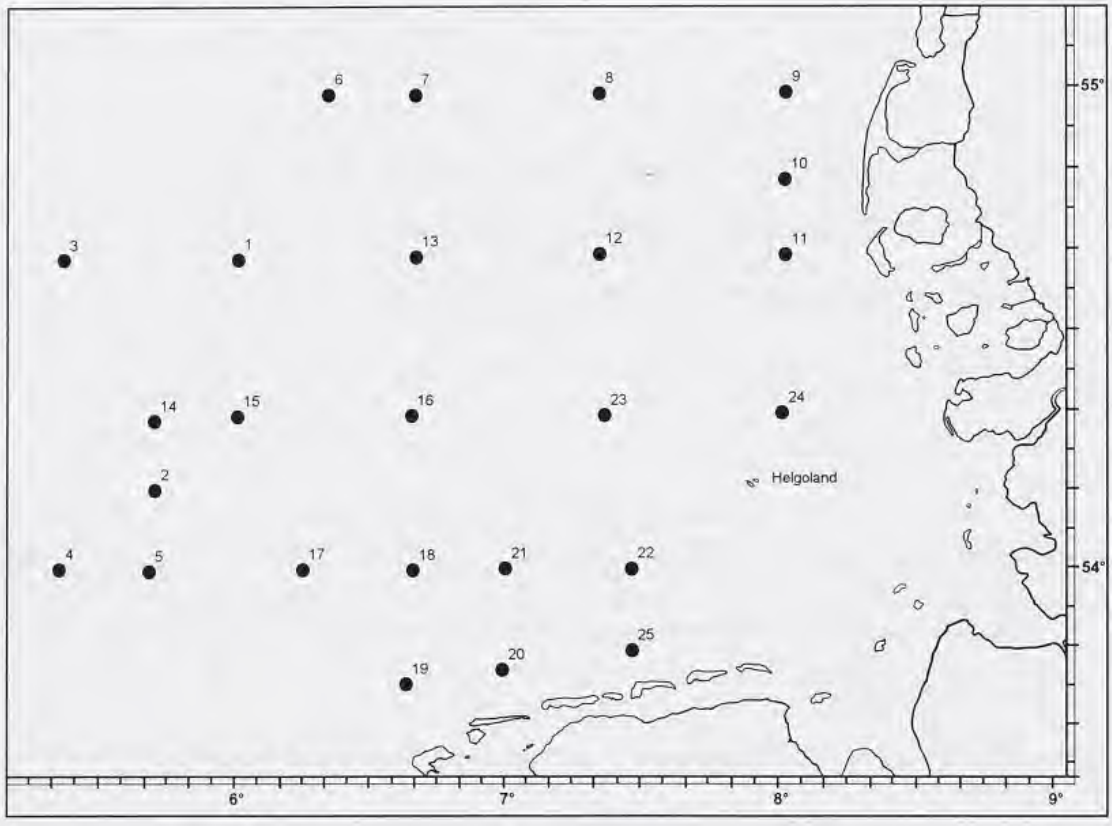



FIG. 1. — Map of stations of the DEB 1987 expedition.

## MATERIALS AND METHODS

The DEB 1987 sampling sites are given in Table 1 and Figure 1. The sampling was done with a van Veen grab (0.2 $m^2$), beam trawl (2 m wide, 1 cm mesh size in cod end), and ring dredge (1 m diameter, 1 cm mesh size). Twenty-four, 21, and 6 samples, respectively, were taken with these samplers; three stations were sampled with all three gear (Table 1). Trawling was usually carried out for 20 minutes at each station (except stn. 6 [21'] and stn. 7 [26']) at 1-2 knots after the gear had reached the bottom. An area of about 1 nautical mile length and 2 m width was covered with each trawl. Samples were sieved through 0.63 mm mesh size and fixed in 10 % formaldehyde. In the laboratory, polychaetes were determined to species level whenever possible (Table 2).

Faunistic attributes were analyzed separately for both types of samples. Van Veen grab samples are more comparable than beam trawl samples, since the beam trawl passes through different patches of the sea floor which may obliterate differences between benthic assemblages. Therefore, only those samples taken with the grab were considered here. We used the statistical package for comparing marine samples, PRIMER ver. 3.1 (GRAY *et al.*,

Source : MNHN, Paris

1988; MED POL, 1992a, b), to compute the following univariate indices: N (the number of individuals in the sample), S species richness (the number of species in a sample), H' species diversity (the Shannon-Wiener information index computed to the base e), and J' the evenness corollary of the Shannon-Wiener index.

TABLE 1. — List of stations of North Sea expedition to German Bight DEB 1978

| Station | Date V 1987 | Depth (m) | Sampling gear[1/] | Coordinates Latitude | Longitude | Silt/Clay[2/] (%) | Sand-grain size[2/] (µm) | Rank[3/] |
|---|---|---|---|---|---|---|---|---|
| 1 | 24 | 43 | Bt, vV | 54°39,9'N | 6°00'E | 5-10 | 63-250 | 2 |
| 2 | 24 | 44 | Bt, vV | 54°10'N | 5°39,5'E | n.d.[5/] | n.d. | n.d. |
| 3 | 24 | 46 | Bt, vV, Rd | 54°40'N | 5°20'E | n.d. | n.d. | n.d. |
| 4 | 24 | 43 | Bt, vV | 54°00'N | 5°20'E | n.d. | n.d. | n.d. |
| 5 | 24 | 44 | Bt, vV | 54°00,03'N | 5°40,02'E | n.d. | n.d. | n.d. |
| 6 | 24 | 46 | Bt, vV | 55°00,02'N | 6°20,02'E | 11-20 | 63-250 | 1 |
| 7 | 24 | 41 | vV, Rd[4/] | 55°00'N | 6°40,1'E | <5 | 63-250, + | 3 |
| 8 | 24 | 31 | Bt, vV | 55°00'N | 7°20'E | <5 | 63-250 | 3 |
| 9 | 24 | 17 | Bt, vV | 55°00,01'N | 8°00,01'E | <5 | 63-250, 500-2000 | 6 |
| 10 | 24 | 16 | Bt, vV | 45°50'N | 8°00'E | <5 | 500-2000 | 7 |
| 11 | 24 | 14 | vV | 54°40'N | 8°00,02'E | <5 | 500-2000 | 7 |
| 12 | 25 | 25 | Bt, vV | 54°39,9'N | 7°20,0'E | <5 | 63-250, 500-2000 | 6 |
| 13 | 25 | 40 | Bt, vV | 54°40'N | 6°39,5'E | 5-10 | 63-250 | 2 |
| 14 | 25 | 42 | Bt, vV | 54°20,02'N | 5°40'E | n.d. | n.d. | n.d. |
| 15 | 25 | 41 | Bt, vV | 54°20,02'N | 6°00,2'E | 5-10 | 63-250 | 2 |
| 16 | 25 | 38 | Bt, vV | 54°20'N | 6°40E | 5-10 | 63-250 | 2 |
| 17 | 25 | 33 | Bt, vV,Rd | 54°00,04'N | 6°16'E | <5 | 63-250, 250-500 | 4 |
| 18 | 25 | 29 | Bt, vV | 54°00,01'N | 6°40,02'E | 5-10 | 63-250 | 2 |
| 19 | 25 | 25 | Bt, vV, Rd | 53°45,04'N | 6°37,03'E | <5 | 500-2000 | 7 |
| 20 | 26 | 18 | vV | 53°47'N | 7°03'E | <5 | 250-500 | 5 |
| 21 | 26 | 30 | Bt, vV | 54°00'N | 6°59,9'E | <5 | 63-250 | 3 |
| 22 | 26 | 36 | Bt, vV | 54°02'N | 7°30'E | 5-10 | 63-250 | 2 |
| 23 | 26 | 43 | Bt, vV | 54°20,01'N | 7°20,01'E | 5-10 | 63-250 | 2 |
| 24 | 26 | 22 | Bt, Rd | 54°20,01'N | 8°00,01'E | <5 | 500-2000 | 7 |
| 25 | 26 | 19 | vV | 53°49,5'N | 7°29'E | <5 | 63-250, 250-500 | 4 |

1/ Bt (beam trawl); vV (van Veen grab); Rd (ring dredge). 2/ According to information in FIGGE, 1981. +: gravel. 3/ Ranked from 1-7 (class 7 with largest sand grain size 500-2000 µm; class 6 with largest sand grain size 500-2,000 µm and also with smaller grains; class 5 with sand grain size 250-500 µm; class 4 with sand grain size 250-500 µm and also with smaller grains; class 3 with sand grain size 63-250 µm; class 2 with sand grain size 63-250 µm and also with 5-10% clay; class 1 with sand grain size 63-250µm and also with 11-20% clay). 4/ Two samples. 5/ n.d.: no data available, i. e., station not on sediment map.

A one-way analysis of variance (ANOVA) was done of S and H' against depth using the Statgraphics package to test the hypothesis that faunal attributes reflect depth. The DEB 1987 sampling program did not encompass replicate sampling; thus, for ANOVA, samples were sorted into four depth classes (I: 14-19 m, II: 20-29 m, III: 30-39 m, and IV: 40-46 m), regardless of their location. Members of a depth class served as "replicates".

To discriminate between samples on the basis of their faunistic attributes, we used the PRIMER package to carry out hierarchical agglomerated classification based on the Bray-Curtis similarity coefficient calculated on square root transformed abundances, employing group average sorting (GRAY *et al.*, 1988). An ordination analysis, multidimensional scaling (MDS), which expresses the rank order of the dissimilarities was done based on the ranked Bray-Curtis similarity matrix and plotted with the superimposed scaled environmental variables of depth and substrate type (MED POL, 1992a, b; GRAY *et al.*, 1992). Van Veen samples 3 and 5 seemed to prevent other samples from clustering, i.e. they are "degenerate samples"; according to accepted practise they were omitted from the respective analyses (MED-POL, 1992a, b; M.R. CARR, pers. comm.). A non-parametric analysis of variance was used to compare the Bray-Curtis similarities with the depth categories.

Source : MNHN, Paris

TABLE 2.— Distribution of taxa in samples. All gears. N° of individuals taken for each depth category (% of samples at each depth category containing species in question)

| Depth: Number of samples: Species | Gear | 14-19 m 7 | 20-29 m 9 | 30-39 m 11 | 40-46 m 24 | Total: = 51 |
|---|---|---|---|---|---|---|
| APHRODITIDAE | | | | | | |
| *Aphrodite aculeata* Linné, 1761 | vV,Bt,Rd[1/] | - | 1 (11.2) | 8 (36.4) | 69 (45.8) | 78 (31.4) |
| POLYNOIDAE | | | | | | |
| *Lepidonotus squamatus* (Linné, 1767) | Bt | - | - | 1 (9.1) | - | 1 (2) |
| *Harmothoe antilopes* McIntosh, 1876 | Bt | - | - | - | 1 (4.2) | 1 (2) |
| *Harmothoe imbricata* (Linné, 1767) | Bt | - | - | 2 (9.1) | 1 (4.2) | 3 (3.9) |
| *Harmothoe lunulata* (Delle Chiaje, 1841) | vV | - | - | 3 (18.2) | - | 3 (3.9) |
| *Harmothoe longisetis* (Grube, 1863) | vV | - | - | - | 2 (8.4) | 2 (3.9) |
| *Harmothoe (Eunoe) nodosa* (Sars, 1860) | vV, Bt | - | - | 3 (18.2) | 19 (25) | 22 (15.7) |
| *Polynoe (Enipo) kinbergi* Malmgren, 1865 | vV | - | - | - | 4 (16.7) | 4 (7.8) |
| SIGALIONIDAE | | | | | | |
| *Pholoe minuta* (Fabricius, 1780)[2/] | vV, Bt | - | 3 (22.3) | 17 (18.2) | 163 (41.7) | 183 (27.5) |
| *Sthenelais limicola* (Ehlers, 1864) | vV, Bt | - | - | 1 (9.1) | 10 (16.7) | 11 (9.8) |
| PISIONIDAE | | | | | | |
| *Pisione remota* (Southern, 1914) | Bt | - | 1 (11.2) | - | - | 1 (2) |
| PHYLLODOCIDAE | | | | | | |
| *Eteone longa* (Fabricius, 1780) | vV | - | 1 (11.2) | - | - | 1 (2) |
| *Eteone foliosa* Quatrefages, 1865 | vV | - | - | - | 1 (4.2) | 1 (2) |
| *Phyllodoce groenlandica* (Oersted, 1842) | Bt | - | 1 (11.2) | - | - | 1 (2) |
| *Eumida sanguinea* (Oersted, 1843) | vV, Bt | 9 (28.6) | 3 (11.2) | 33 (54.5) | 1 (4.2) | 46 (19.6) |
| HESIONIDAE | | | | | | |
| *Ophiodromus flexuosus* (Delle Chiaje, 1822) | vV, Bt | - | - | 1 (9.1) | 7 (16.7) | 8 (9.8) |
| PILARGIDAE | | | | | | |
| *Synelmis klatti* (Friedrich, 1950) | vV | - | - | - | 1 (4.2) | 1 (2) |
| SYLLIDAE | | | | | | |
| *Eusyllis blomstrandi* Malmgren, 1867 | Bt | - | 1 (11.2) | - | - | 1 (2) |
| *Autolytus langerhansi* Gidholm, 1967 | Bt | - | - | - | 1 (4.2) | 1 (2) |
| *Autolytus edwarsi* Saint Joseph, 1887 | Bt | - | - | 1 (9.1) | 221 (16.7) | 222 (9.8) |
| NEREIDIDAE | | | | | | |
| *Nereis zonata* Malmgren, 1867 | Bt | - | - | - | 1 (4.2) | 1 (2) |
| *Nereis (E.) longissima* Johnston, 1840 | vV | - | - | - | 1 (4.2) | 1 (2) |
| NEPHTYIDAE | | | | | | |
| *Nepthys cirrosa* Ehlers, 1868 | vV | 4 (14.3) | - | 2 (9.1) | - | 6 (3.9) |
| *Nephtys hombergii* Savigny, 1818 | vV, Bt, Rd | 7 (14.3) | 2 (11.2) | 11 (36.4) | 15 (37.5) | 35 (29.4) |
| *Nephtys incisa* Malmgren, 1865 | vV | - | - | - | 3 (12.5) | 3 (5.9) |
| *Nephtys caeca* (Fabricius, 1780) | vV, Bt, Rd | 5 (57.1) | 6 (45) | 2 (18.2) | 1 (4.2) | 14 (21.6) |
| *Nephtys longosetosa* Oersted, 1843 | vV, Rd | 8 (57.1) | 25 (45) | 5 (9.1) | 6 (8.4) | 44 (21.6) |
| *Nepthys assimilis* Oersted, 1843 | vV, Bt | 1 (14.3) | - | 2 (18.2)) | 8 (20.8) | 11 (15.7) |
| GLYCERIDAE | | | | | | |
| *Glycera rouxii* Aud.& M.-Edwards, 1833 | vV | - | - | - | 7 (8.4) | 7 (3.9) |
| *Glycera alba* (O. F. Müller, 1776) | vV, Bt | - | - | - | 13 (20.8) | 13 (9.8) |
| GONIADIDAE | | | | | | |
| *Glycinde nordmanni* (Malmgren, 1865) | vV, Bt | - | - | - | 6 (16.7) | 6 (7.8) |
| *Goniada maculata* Oersted, 1843 | vV | - | - | 3 (27.3) | 1 (4.2) | 4 (7.8) |
| *Goniadella bobretzkii* (Annenkova, 1929) | vV, Bt | 3 (42.9) | 1 (11.2) | - | 2 (8.4) | 6 (11.8) |
| LUMBRINERIDAE | | | | | | |
| *Lumbrineris* cf. *gracilis* (Ehlers, 1868) | vV, Bt | - | 1 (11.2) | - | 3 (12.5) | 4 (7.8) |
| *Lumbrineris* type A | vV | - | - | - | 2 (8.4) | 2 (3.9) |

Source : MNHN, Paris

TABLE 2 (continued)

| Depth: Number of samples: Species | Gear | 14-19 m 7 | 20-29 m 9 | 30-39 m 11 | 40-46 m 24 | Total: = 51 |
|---|---|---|---|---|---|---|
| ORBINIIDAE | | | | | | |
| *Scoloplos armiger* (O. F. Müller, 1776) | vV, Bt | 52 (71.4) | 22 (22.3) | 45 (45.5) | 42 (29.2) | 161 (37) |
| PARAONIDAE | | | | | | |
| *Paraonis gracilis* (Tauber, 1879) | vV | - | - | - | 3 (4.2) | 3 (2) |
| POECILOCHAETIDAE | | | | | | |
| *Poecilochaetus serpens Allen, 1904* | vV | - | - | 1 (9.1) | 3 (8.4) | 4 (5.9) |
| SPIONIDAE | | | | | | |
| *Spio filicornis* (O. F. Müller, 1776) | vV | - | - | 4 (9.1) | - | 4 (2) |
| *Polydora ciliata* (Johnston, 1838) | Bt | - | - | - | 1 (4.2) | 1 (2) |
| *Scolelepis bonnieri* (Mesnil, 1896) | vV | 2 (14.3) | 2 (22.3) | 6 (36.4) | 1 (4.2) | 11 (15.7) |
| *Spiophanes kröyeri* Grube, 1860 | vV | - | - | - | 1 (4.2) | 1 (2) |
| *Spiophanes bombyx* (Claparède, 1870) | vV | 9 (57.1) | 4 (33.6) | 33 (18.2) | 51 (37.5) | 97 (35.3) |
| *Aonides paucibranchiata* Southern, 1914 | vV, Bt | - | 2 (11.2) | 7 (27.3) | 1 (4.2) | 10 (9.8) |
| MAGELONIDAE | | | | | | |
| *Magelona alleni* Wilson, 1958 | vV | - | - | - | 1 (4.2) | 1 (2) |
| *Magelona mirabilis* (Johnston, 1865) | vV, Bt | 37 (42.9) | 12 (33.6) | 20 (18.2) | 25 (20.8) | 94 (25) |
| *Magelona* type A | vV | 1 (14.3) | - | 3 (18.2) | 3 (8.4) | 7 (9.8) |
| *Magelona* type B | vV | - | - | - | 3 (12.5) | 3 (5.9) |
| *Magelona* type C | vV | - | - | - | 3 (8.4) | 3 (3.9) |
| CHAETOPTERIDAE | | | | | | |
| *Chaetopterus variopedatus* (Renier, 1804) | vV | - | - | - | 5 (8.4) | 5 (3.9) |
| FLABELLIGERIDAE | | | | | | |
| *Diplocirrus glaucus* (Malmgren, 1867) | vV | 1 (14.3) | - | - | 12 (12.5) | 13 (7.8) |
| CIRRATULIDAE | | | | | | |
| *Chaetozone setosa* Malmgren, 1867 | vV, Bt | 4 (28.6) | 7 (22.3) | 9 (36.4) | 21 (29.2) | 41 (29.4) |
| *Dodecaceria concharum* Oersted, 1843 | vV, Bt | - | 10 (22.3) | - | - | 10 (3.9) |
| SCALIBREGMATIDAE | | | | | | |
| *Polyphysia crassa* (Oersted, 1843) | Bt | - | - | - | 1 (4.2) | 1 (2) |
| *Scalibregma inflatum* Rathke, 1843 | vV | - | - | - | 1 (4.2) | 1 (2) |
| OPHELIIDAE | | | | | | |
| *Ophelia limacina* (Rathke, 1843) | vV, Bt, Rd | 37 (42.9) | 88 (67) | 25 (36.4) | 10 (16.7) | 160 (33.4) |
| *Ophelina acuminata* Oersted, 1843 | vV | - | - | 1 (9.1) | 2 (8.4) | 3 (5.9) |
| CAPITELLIDAE | | | | | | |
| *Capitella capitata* (Fabricius, 1870) | Bt | - | - | - | 2 (4.2) | 2 (2) |
| *Notomastus latericeus* Sars, 1851 | vV | - | - | - | 4 (8.4) | 4 (3.9) |
| OWENIIDAE | | | | | | |
| *Owenia fusiformis* Delle Chiaje, 1841 | vV, Bt, Rd | - | - | - | 16 (20.8) | 16 (9.8) |
| PECTINARIIDAE | | | | | | |
| *Pectinaria belgica* (Pallas, 1766) | Bt | - | - | - | 1 (4.2) | 1 (2) |
| *Pectinaria koreni* Malmgren, 1865 | vV, Bt, Rd | - | - | 1 (9.1) | 44 (33.4) | 45 (17.6) |
| *Pectinaria auricoma* (O. F. Müller, 1776) | vV, Bt, Rd | - | - | - | 52 (33.4) | 52 (15.7) |
| AMPHARETIDAE | | | | | | |
| *Ampharete finmarchica (Sars, 1864)* | vV | - | 1 (11.2) | - | 17 (12.5) | 18 (7.8) |
| TEREBELLIDAE | | | | | | |
| *Lanice conchilega* (Pallas, 1776) | vV, Bt | 3 (14.3) | - | 7 (18.2) | - | 10 (5.9) |
| *Lysilla loveni* Malmgren, 1865 | vV, Bt | - | - | - | 6 (20.8) | 6 (9.8) |
| SABELLIDAE | | | | | | |
| *Sabella penicillus* Linné, 1767 | vV, Bt | - | - | - | 2 (8.4) | 2 (3.9) |

1/ vV = van Veen grab, Bt = beam trawl, Rd = ring dredge. 2/ sensu HARTMANN-SCHRÖDER (1971).

Source : MNHN, Paris

Analysis of samples with respect to the sediment was done by cluster analysis. The information on substrate grain size is from a map, "Sedimentverteilung in der Deutschen Bucht" (FIGGE, 1981) (Table 1). Sediment was divided into 7 classes ranked by decreasing size (for raw data and ranks see Table 1). A correlation between depth and substrate classes was made.

## RESULTS AND DISCUSSION

Polychaetes were analyzed from 51 samples taken at 25 stations and covered a depth range from 14 to 46 m. There were about 1,500 specimens in 46 genera and 29 families. Sixty-seven species were determined of which 63 were identified to species (Table 2).

For analysis of depth distributions samples were arbitrarily grouped into four depth categories. Fourteen species were present in the entire depth range, including the most frequently encountered species; these were, *Scoloplos armiger, Spiophanes bombyx* and *Ophelia limacina*, which were present in >30 % of the samples; *Nephtys hombergii, N. caeca, N. longosetosa, Magelona mirabilis* (presumably mistaken for *M. papillicornis* previously, see JONES, 1977) and *Chaetozone setosa*, which were present in 20-30 % of the samples; *Eumida sanguinea, Nepthys assimilis, Goniadella bobretzkii, Scolelepis bonnieri*, which were present in 10-19 % of the samples. Two species, *Magelona* type A and *Diplocirrus glaucus*, were present in all the depth ranges sampled but present in fewer than 10 % of the samples. Among the abundant species, *Aphrodite aculeata* and *Pholoe minuta* (>20 % of the samples), were found only below the depth of 20 m; *Harmothoe (Eunoe) nodosa, Pectinaria koreni* and *Pectinaria auricoma* (10-19 %) were found only below the depth of 30 m. Altogether, five species were found only at depths less than 30 m (*Pisione remota, Eteone longa, Eusyllis blomstrandi, Phyllodoce groenlandica, Dodecaceria concharum*), whereas 32 species were found only at depths greater than 30 m, with 29 of these present only at depths greater than 40 m (Table 2).

Seventy-six percent of the species, i.e., 51, were found in fewer than 10 % of the samples and are thus comparatively rare (Table 2). The six most abundant species were *Autolytus edwarsi, Pholoe minuta, Scoloplos armiger, Ophelia limacina, Spiophanes bombyx*, and *Magelona mirabilis*. These comprised 8.9 % of all species. The large species, *Aphrodite aculeata*, was also abundant in deeper waters with 78 individuals (Table 2). Fifteen species (22.4 % of the total) were represented by 11-55 individuals. Eighteen species (26.9 %) were represented by two individuals and 18 species (26.9 %) by only one.

ZIEGELMEIER (1978) found that about two-thirds of all polychaetes sampled belonged to *Spiophanes bombyx, Magelona papillicornis*, and *Scoloplos armiger*. *Magelona papillicornis* also was the most common species in the study of RACHOR & GERLACH (1978). *Magelona papillicornis* in both these studies was probably *M. mirabilis* (see JONES, 1977).

Table 2 lists the gear used to collect the material. Most of the individuals of *Aphrodite aculeata* and some additional polychaetes such as polynoids were taken with the beam trawl. *Spiophanes bombyx* was only collected with the grab. The number of polychaete species per sample was 3 to 26 for the van Veen collections, 1 to 18 for beam trawl collections, and 1 to 4 for the ring dredge collections (Table 3).

Comparison of the mean species richness S indicated an increase with increasing depth (7.2 ± 4.0 in depth class I, 8.0 ± 4.6 in depth class II, 13.0 ± 6.6 in depth class III, and 11.4 ± 6.3 in depth class IV for the van Veen grab samples). However, an ANOVA test, carried out with the data from the van Veen grabs found that the difference in number of species with depth was not statistically significant. The species diversity index, H', also increased with depth (Table 3); while the ANOVA test for significance with H' calculation was higher than for S, the difference between the depth classes with H' was not significant ($p > 0.05$; d.f. 3.47). The richest van Veen sample was number 6 from a high fraction of clay at 46 m with 26 species and the highest species diversity (H'= 2.9) (Table 1). According to HARTMANN-SCHRÖDER (1971), species found at this station either prefer muddy substrate or are not known to have any substrate preference. STRIPP (1969) and KÜNITZER (1990) also found that species richness, respectively number of individuals of macro- and meiofauna, increased from coarse to fine sediment. Regarding only the van Veen collections of this study, those with the fewest species include stations 9 and 19 at a depth of 17-25 m (3-4 species each). These stations had the largest substrate grain size. However, there were also stations with few species in deeper waters with fine grain size (stations 7 and 14, 41 and 42 m, respectively). According to ZIEGELMEIER (1978) the poorest stations with lowest biomass were situated close to the coast of Schleswig-Holstein, which he attributed to the fine to coarse sand, which is very mobile due to the strong tidal currents in this area. Among the stations of the present study sampled with vV, 9, 10 and 11 are aligned with 8°E along the coast of Schleswig-Holstein in quite shallow water. They belong to those with the largest substrate grain size. Stations 9 and 11 show low species diversity (three and four species, respectively).

Source : MNHN, Paris

Station 10 is also very shallow, and has the same substrate as the other two but shows a higher diversity (8 species). According to HARTMANN-SCHRÖDER (1971), species found at these stations either prefer sandy substrate (*Goniadella bobretzkii*, *Spiophanes bombyx*, and *Ophelia limacina*) or are not known to have any preference (*Nephtys caeca*, *N. longosetosa*, and *Scoloplos armiger*).

TABLE 3. — Number of individuals (N), species richness (S), species diversity (H') and evenness (J') in individual samples.

| | Gear | | van | Veen | | beam | trawl | ring | dredge |
|---|---|---|---|---|---|---|---|---|---|
| Station | Depth (m) | N | S | H' | J' | N | S | N | S |
| **A (≤ 19m)** | | | | | | | | | |
| 11 | 14 | 21 | 4 | 0.695 | 0.494 | - | - | - | - |
| 10 | 16 | 28 | 8 | 1.589 | 0.768 | 3 | 2 | - | - |
| 9 | 17 | 41 | 3 | 0.629 | 0.572 | 2 | 1 | - | - |
| 20 | 18 | 16 | 8 | 1.836 | 0.883 | - | - | - | - |
| 25 | 19 | 58 | 13 | 1.718 | 0.670 | - | - | - | - |
| **B (20-29m)** | | | | | | | | | |
| 24 | 22 | - | - | - | - | 4 | 3 | 1 | 1 |
| 12 | 25 | 21 | 7 | 1.325 | 0.681 | 18 | 8 | 7 | 1 |
| 19 | 25 | 17 | 4 | 1.038 | 0.748 | 2 | 2 | 83 | 3 |
| 18 | 29 | 88 | 13 | 1.470 | 0.573 | 1 | 1 | - | - |
| **C (30-39m)** | | | | | | | | | |
| 21 | 30 | 25 | 12 | 2.256 | 0.908 | 5 | 2 | - | - |
| 8 | 31 | 121 | 13 | 1.916 | 0.747 | 7 | 3 | - | - |
| 17 | 33 | 33 | 7 | 1.189 | 0.664 | 2 | 2 | 4 | 2 |
| 22 | 36 | 14 | 9 | 1.965 | 0.894 | 18 | 4 | - | - |
| 16 | 38 | 11 | 24 | 2.073 | 0.900 | 7 | 5 | - | - |
| **D (≥40 m)** | | | | | | | | | |
| 13 | 40 | 45 | 17 | 2.630 | 0.928 | 7 | 2 | - | - |
| 7 | 41 | 9 | 4 | 1.215 | 0.876 | - | - | - | - |
| 15 | 41 | 91 | 10 | 1.089 | 0.473 | 2 | 2 | - | - |
| 14 | 42 | 4 | 4 | 1.386 | 1.000 | 7 | 2 | - | - |
| 1 | 43 | 28 | 10 | 2.004 | 0.870 | 21 | 7 | - | - |
| 4 | 43 | 47 | 10 | 1.644 | 0.714 | 8 | 2 | - | - |
| 23 | 43 | 74 | 15 | 2.014 | 0.785 | 18 | 9 | - | - |
| 2 | 44 | 14 | 11 | 2.305 | 0.961 | 6 | 1 | - | - |
| 5 | 44 | 53 | 11 | 1.897 | 0.791 | 10 | 7 | - | - |
| 3 | 46 | 12 | 7 | 1.699 | 0.873 | 7 | 4 | 16 | 4 |
| 6 | 46 | 78 | 26 | 2.866 | 0.890 | 347 | 18 | - | - |
| No. of indiv. (Total N=1562) | | 949 | | | | 502 | | 111 | |

Depth frequently correlates with substrate characteristics as indicated by THORSON (1957) and HYLLEBERG & NATEEWATHANA (1984). We looked for indications that this might apply to the present material. First we considered the relationship between the depth classes and substrate grain size and found them to be positively correlated ($r = 0.641$, d.f. 20, $p < 0.01$). There was a significant relationship between the depth classes and the ranked grain size classes (one way ANOVA, $p < 0.01$, d.f. 3.18). Actually, there was very little difference between the mean grain size ranks of the first two depth classes ($5.8 \pm 1.3$, $5.5 \pm 2.4$, $2.8 \pm 0.8$, $2.1 \pm 0.7$).
Next we conducted a cluster analysis for faunistic similarity between samples. The dendrogram of the van Veen samples (Fig. 2a), showed three clusters (marked A, B, and C). Cluster A comprises samples only from depth category IV, cluster B comprises some samples from depth category IV and all the samples from depth category III, while cluster C comprises all vV samples from depth categories II and I. The dendrogram thus broadly classifies the samples according to the depth categories and, similarly, according to the substrate size. The corresponding 2-dimensional ordination plots based on the Bray-Curtis similarities with superimposed depth (Fig. 2b) and substrate grain size (Fig. 2c) show this clearly. An indication of the goodness of fit of the plot is given by its stress value

Source : MNHN, Paris

(an expression of the deformation necessary to transform the model from a 3-dimensional one to a 2-dimensional one); the lowest stress value for the van Veen MDS plot was 0.172 (0.182, 0.218). Lower stress values (0.1) would indicate a more accurate presentation of the samples (M.R. CARR, pers. comm.). Due to these somewhat higher stress values, we must conclude that the plots of the samples' Bray-Curtis similarity based on their faunal attributes is a fair (rather than an excellent) representation, and it reflects the correspondence between the faunistic attributes of the samples and their depth distributions as well as the grain size parameters. The correspondence with both these parameters is most obvious for cluster C - the shallowest samples with the coarsest grains - but also holds true for cluster A with the finest grain size (Fig. 2b-c). The non-parametric analysis of similarity *vis a vis* depth for the van Veen samples showed significant differences ($p < 0.05$) only between samples less than 20 m deep and those deeper than 40 m. The fact that the grain size data was obtained from a map, and not from analysis of substrate collected with the samples must introduce error, the extent of which we cannot know. The impact of any local sediment patchiness on the faunal attributes actually measured cannot be determined. Presumably, the actual correspondence with substrate is better than that shown on the plot.

The van Veen samples contained 80.5 % of the 67 species collected by the expedition. The nature of the samples themselves with as many as 50 % of the species represented by only one individual contributed to the low similarities between samples (Fig. 2a). For greater significance, larger samples or replicate sampling with similarities computed on the mean abundance data has been suggested (M.R. CARR, pers. comm.)

Among the common species, some occur in considerably higher numbers in certain samples than in the others (*Aphrodite aculeata*, *Pholoe minuta*, *Scoloplos armiger*, *Spiophanes bombyx*, *Magelona mirabilis*, *Ophelia limacina*) (Table 4). Station 6 was the richest in species and in number of individuals with both the van Veen and the beam trawl samplers. At this station *Autolytus edwarsi* was found in large numbers, but it was not collected at many stations (Table 4).

TABLE 4. — Species of DEB 1978 found in great number (% of individuals = % of all individuals of this species taken at all stations)

| Species | Sample/Gear | No. of individuals | % of individuals |
|---|---|---|---|
| *Aphrodite aculeata* | 6Bt | 32 | 41 |
| *Pholoe minuta* | 15vV | 61 | 34 |
| | 6Bt | 40 | 22 |
| *Scoloplos armiger* | 8vV | 37 | 23 |
| | 9vV | 33 | 20.5 |
| *Spiophanes bombyx* | 8vV | 32 | 33 |
| *Magelona mirabilis* | 23vV | 20 | 21.3 |
| | 25vV | 30 | 32 |
| *Ophelia limacina* | 19Rd | 59 | 36.9 |
| *Autolytus edwarsi* | 6Bt | 213 | 95 |

Although the stations overlapped with some of those sampled by HARTMANN-SCHRÖDER & STRIPP (1968), it is not possible to compare species composition and abundances between the two studies since a smaller sieve mesh size was used by them. HARTMANN-SCHRÖDER & STRIPP (1968) included some meiobenthic species lacking in the present study, which might have been lost because of the greater mesh size used here: *Hesionura augeneri*, *Microphthalmus similis*, *M. listensis*, *Sphaerosyllis hystrix*, *S. tetralix*, but also *Anaitides subulifera*, *Eumida bahusiensis*, *E. punctifera*, *Polydora (Pseudopolydora) pulchra*, and *Tharyx marioni*. Among the common species mentioned by HARTMANN-SCHRÖDER & STRIPP (1968), *Sthenelais limicola*, *Goniadella bobretzkii*, *Scolelepis bonnieri*, *Aonides paucibranchiata*, and *Ampharete finmarchica* were found in the present DEB sampling but in no more than 7-16% of the samples.

Among the interesting species collected by the expedition, *Lysilla loveni* (DEB-stations 1, 2, 6, and 15) has only been found twice earlier in the North Sea, i.e., off Oostende/Belgium (Channel) and close to the Norwegian Trough (HARTMANN-SCHRÖDER & STRIPP, 1968). According to MICHAELSEN (1897), this species does not occur in the North Sea proper, but in the Skagerrak, Kattegat, the Sound, and the Belts. HOLTHE (1985) showed a map with the location of living specimens which were primarily from the Scandinavian coast. The type locality is Bohuslän/ Sweden.

Source : MNHN, Paris

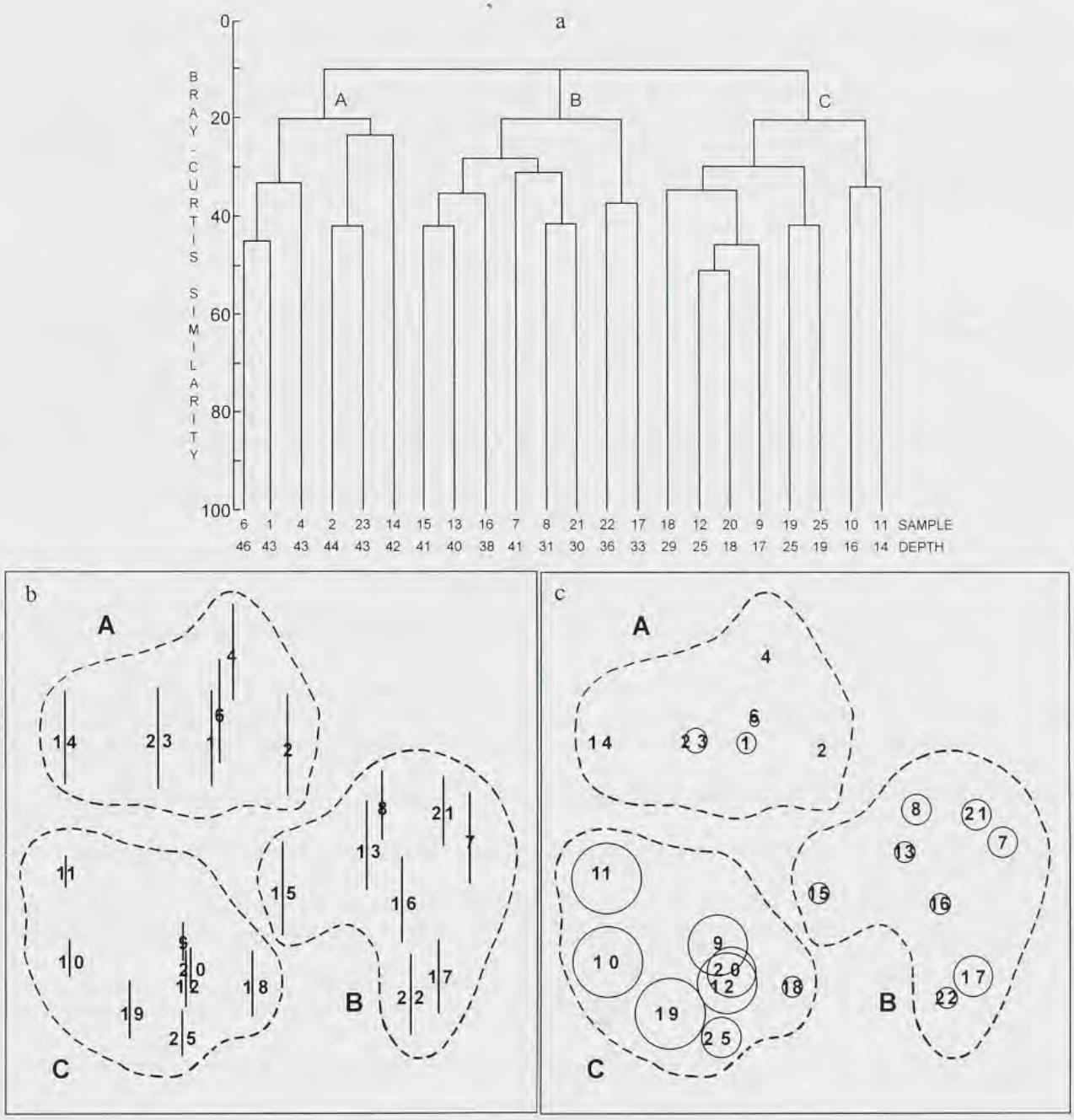



FIG. 2. — DEB 1987 van Veen samples (stations 3 and 5 omitted). a. Classification analysis of polychaete data from DEB 1987 expedition (square root-transformed data with Bray-Curtis dissimilarities). The sample numbers and corresponding depths are shown on the abscissa. b and c. MDS ordination plot of the same data with grouping showing clustering of samples based on species faunistic attributes and with superimposed corresponding scaled environmental parameters. b: depth of samples. The shallowest samples with the shortest lines (cluster C); the deepest samples (cluster A) with the longest lines. c: substrate grain size. The sediment was ranked into seven classes (see Table 1). The largest circles (cluster C) represent the coarsest grain size.

Source : MNHN, Paris

In conclusion, the depth range sampled was sufficiently broad to identify differences in the distribution of some species. The faunal attributes separated broadly both by depth and by substrate type. The selected depth categories were found to comprise some mixture of the substrate categories. Since the German Bight is surrounded by rivers which carry sediment, substrate categories are not only a simple matter of depth. In order to determine whether depth or substrate is controlling the species attributes, it would be of interest to compare the classification of samples according to their granulometry with that obtained from classifying by depth. However, this comparison can only be done if the granulometry is determined from sediment collected with the sample. Since depth and substrate grain size are highly correlated, it is difficult to distinguish which of these factors is the most important one in controlling the distribution of the species. Moreover, some of the present differences may be artifacts which could be eliminated by additional sampling.

## ACKNOWLEGEMENTS

We thank M. TÜRKAY for the samples of Polychaeta, M.-L. TRITZ (both of the Senckenbergmuseum, Frankfurt) for processing the samples and skillful technical assistance, D. EIBYE-JACOBSEN and M.E. PETERSEN (both of the Zoological Museum, Copenhagen) for taxonomic advice, as well as M.R. CARR (The Plymouth Marine Laboratory) and E. PAPATHANASSIOU (The National Centre for Marine Research, Athens) for discussing the data and for making the PRIMER software available. M.N. BEN-ELIAHU thanks the Senckenberg Museum for enabling a working visit to examine the collections, and the Marine and Coast Environment Division of the Israel Department of the Environment for enabling participation in the FAO/IOC/UNEP Training Workshop MED POL-Phase II on the Statistical Treatment and Interpretation of Marine Community Data at Bar Ilan University. M. TÜRKAY, H.J. BROMLEY, D. GATEÑO, and R. LOTAN read various drafts.

## REFERENCES

BASFORD, D.J., ELEFTHERIOU, A. & RAFFAELLI, D., 1989. — The epifauna of the northern North Sea (56°-61°N). *J. mar. biol. Ass. U.K.*, **69** : 387-407.

FIGGE, K., 1981. — *Sedimentverteilung in der Deutschen Bucht*. 1: 250000 Karte Nr. 2900, Dt. Hydrogr. Inst., Hamburg.

FRAUENHEIM, K., NEUMANN, V., THIEL, H. & TÜRKAY, M., 1989. — The distribution of the larger epifauna during summer and winter in the North Sea and its sensibility for environmental monitoring. *Senckenbergiana marit.*, **20** : 101-118.

FRIEDRICH, H., 1938. — *Die Tierwelt der Nord- und Ostsee. Bd. VIb. Polychaeta*. Akademische Verlagsgesellschaft, Leipzig, 201 pp.

GLÉMAREC, M., 1973. — The benthic communities of the European North Atlantic continental shelf. *Oceanogr. Mar. Biol. Ann. Rev.*, **11** : 263-289.

GRAY, J.S., ASCHAN, M., CARR, M.R., CLARKE, K.R., GREEN, R.H., PEARSON, T., ROSENBERG, R. & WARWICK, R.M., 1988. — Analysis of community attributes of the benthic macrofauna of Frienfjord/Langesund and in a mesocosm experiment. *Mar. Ecol. Progr. Ser.*, **66** : 285-288.

GRAY, J.S., MCINTYRE, A.D. & STIRN, J., 1992. — Manual of Methods in Aquatic Environment Research, part 11-Biological Measurement of Marine Pollution. With a Particular Reference to Benthos. *FAO Fisheries Technical Paper* 324, 48 pp.

HARTMANN-SCHRÖDER, G., 1971. — *Die Tierwelt Deutschlands. 58. Teil. Annelida, Borstenwürmer, Polychaeta*. Gustav Fischer Verlag, 594 pp.

HARTMANN-SCHRÖDER, G. & STRIPP, K., 1968. — Beiträge zur Polychaetenfauna der Deutschen Bucht. *Veröff. Inst. Meeresforsch. Bremerh.*, **11** : 1-24.

HOLTHE, T., 1985. — Polychaeta Terebellomorpha. Marine Invertebrates of Scandinavia No. 7. *Norwegian University Press*, 194 pp.

HYLLEBERG, J. & NATEEWATHANA, A., 1984. — Responses of polychaetes to monsoon and offshore mining associated sediment disturbance. In : P. HUTCHINGS (ed), *Proc. First International Polychaete Conference*. Linnean Society of New South Wales : 279-291.

JONES, M.L., 1977. — A redescription of *Magelona papillicornis* O.F. Müller. In : D. REISH & FAUCHALD, K. (eds), *Essays on polychaetous annelids in memory of Dr. Olga Hartman*. Allan Hancock Foundation, University of Southern California, Los Angeles : 247-266.

Source : MNHN, Paris

KIRKEGAARD, J.B., 1969. — A quantitative investigation of the central North Sea Polychaeta. *Spolia Zool. Mus haun.*, **29** : 1-284.

KÜNITZER, A., 1990. — The infauna and epifauna of the central North Sea. *Meeresforsch.*, **33** : 23-37.

MCINTYRE, A.D., 1978. — The benthos of the western North Sea. *Rapp. P-v. Réun. Cons. int. Expl. Mer,* **172** : 405-417.

MED POL, 1992a. — Lecture notes prepared for the training workshop on the statistical treatment and interpretation of marine community data. Israel, 14-19 June, 1992. MED POL: *Long-term program for pollution monitoring and research in the Mediterranean. Phase II.* FIR/MEDPOL/ISR/3. IOC, UNEP, April 1992, Athens, 148 pp.

MED POL, 1992b. — Practical notes for using the computer programmes prepared for the training workshop on the statistical treatment and interpretation of marine community data. Israel, 14-19 June, 1992. MED POL: *Long-term program for pollution monitoring and research in the Mediterranean. Phase II.* FIR/MEDPOL/ISR/3. IOC, UNEP, April 1992, Athens, 92 pp.

MICHAELSEN, W., 1897. — Die Polychaetenfauna der deutschen Meere einschließlich der benachbarten und verbindenden Gebiete. *Wiss. Meeresunters. dt. Meere.*, **2** : 1-215.

RACHOR, E. & GERLACH, S.A., 1978. — Changes of the macrobenthos in a sublittoral sand area of the German Bight, 1967 to 1975. *Rapp. P-v. Réun. Cons. int. Expl. Mer,* **172** : 418-431.

SALZWEDEL, H., RACHOR, E. & GERDES, D., 1985. — Benthic macrofauna communities in the German Bight. *Veröff. Inst. Meeresforsch. Bremerh.*, **20** : 199-267.

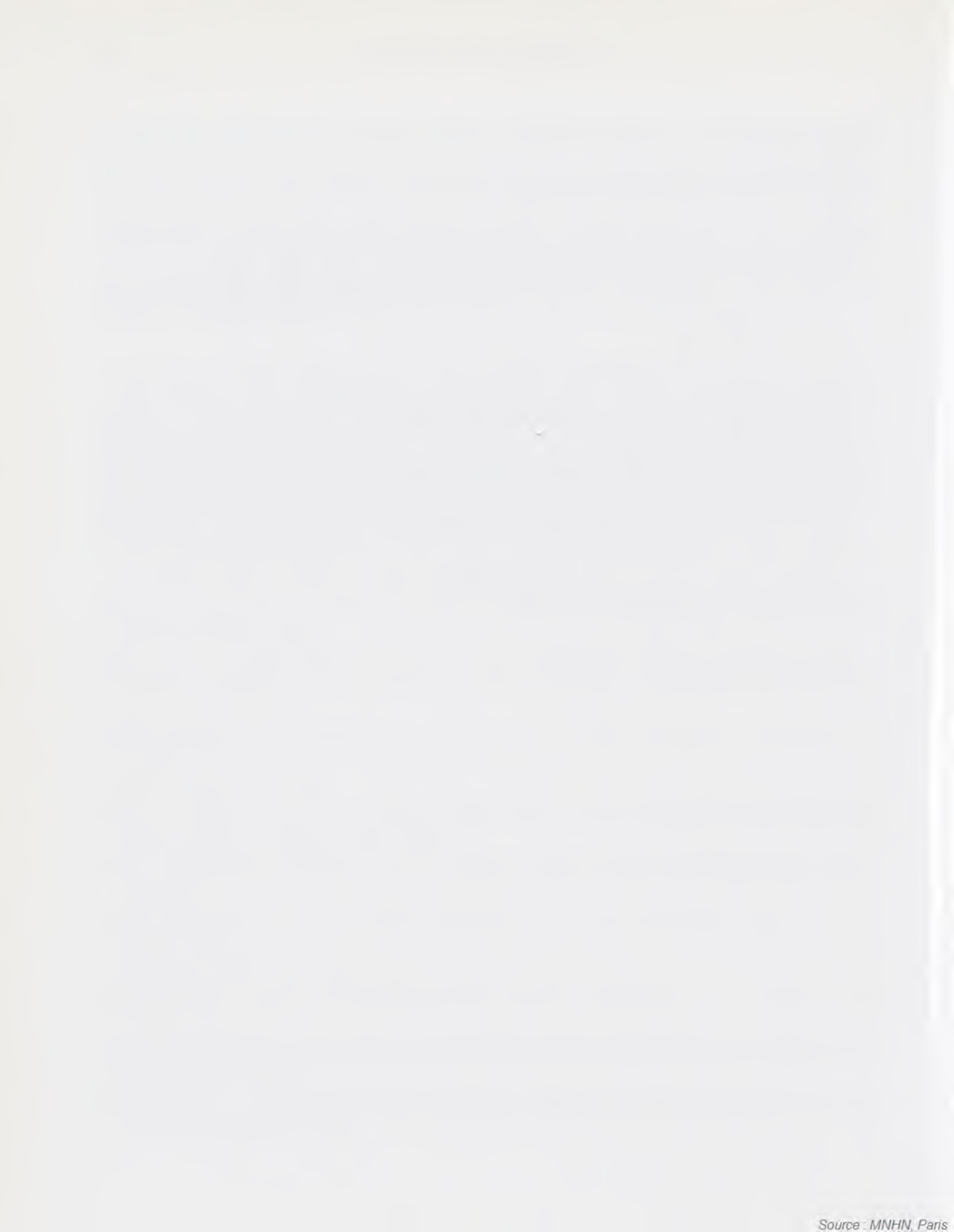
STRIPP, K., 1969. — Die Assoziationen des Benthos in der Helgoländer Bucht. *Veröff. Inst. Meeresforsch. Bremerh.*, **12** : 95-141.

STRIPP, K. , GERLACH, A., 1969. — Die Bodenfauna im Verklappungsgebiet von Industrieabwässern nordwestlich von Helgoland. *Veröff. Inst. Meeresforsch. Bremerh.*, **12** : 149-156.

THORSON, G., 1957. — Bottom communities (sublittoral or shallow shelf). *In*: J. W. HEDGPETH (ed), *Treatise on Marine Ecology and Paleoecology. Vol. 1. Ecology*, Mem. **67**, Geological Society of America, New York : 461-534.

ZIEGELMEIER, E., 1978. — Macrobenthos investigations in the eastern part of the German Bight from 1950 to 1974. *Rapp. P-v. Réun. Cons. int. Expl. Mer*, **172** : 432-444.

Source : MNHN, Paris



Source : MNHN, Paris

# Sélection des grains de sable selon leur nature et leur forme par *Sabellaria alveolata* Linné (Polychète, Sabellariidé) lors de la reconstruction expérimentale de son tube

*Yves GRUET* & Yves BODEUR***

Université de Nantes, 2 rue de la Houssinière
44072 Nantes Cedex, France
* Laboratoire de Biologie Marine
** Laboratoire de Géologie

RÉSUMÉ

En laboratoire, le Polychète *Sabellaria alveolata* a la capacité de reconstruire son tube cassé à la condition de lui en laisser une portion d'au moins 1 cm. Différents types de sédiments, purs ou mélangés, ont été mis à la disposition de vers isolés et élevés dans des conditions comparables. Les taux de reconstruction et les pourcentages des grains utilisés ont été calculés. Les résultats montrent un net refus pour les fragments de moules (très anguleux et allongés) ou encore pour les micas plats et à bords tranchants. Les taux de reconstruction sont très bas pour ces sédiments. Au contraire les vers reconstruisent vite, en présence de sables mixtes parmi lesquels ils choisissent d'abord les grains arrondis ou plus ou moins ovoïdes de quartz et ensuite ceux de feldspath à la micromorphologie plus rugeuse. La forme et la micromorphologie des grains et non leur nature minéralogique, semblent être les facteurs décisifs pour un fort taux de reconstruction.

ABSTRACT

**Shape and compositional selection of sand grains by *Sabellaria alveolata* Linnaeus (Polychaeta, Sabellariidae) in the experimental reconstruction of the tube**

*Sabellaria alveolata* can rebuild its broken tube under laboratory conditions providing there is a least one centimeter present. Sand grains of different types were introduced into dishes containing worms. The rates of tube reconstruction and the percentages of different grains used were calculated. Worms selected more-or-less ovoid quartz or felspathic sand grains and reconstructed their tubes rapidly. On the other hand, worms generally rejected those grains which were either sharp edged mussel shell fragments or thin plated mica. If the worm accepted these latter grains, tube reconstruction rates were low. The shape and the micromorphology of the sand grain seemed to be the deciding factor in selection for reconstruction rather than the chemical nature of the sand grain.

---

GRUET, Y. & Y. BODEUR, 1994. — Sélection des grains de sable selon leur nature et leur forme par *Sabellaria alveolata* Linné (Polychète sabellariidé) lors de la reconstruction expérimentale de son tube. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 425-432. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

L'individu de *Sabellaria alveolata* (Linné), long de 1 à 3 cm, vit à l'intérieur d'un tube formé de deux gaines concentriques : l'une interne, très mince, de nature organique, riche en soufre (VOVELLE, 1965) ; l'autre externe, arénacée, de 2 à 5 mm d'épaisseur de paroi, 6 à 15 mm de diamètre total, et jusqu'à 50 à 70 cm de long. Les grains de sable constituant le tube externe sont collectés dans le milieu environnant au moyen de filaments buccaux (ORRHAGE, 1978), puis triés et englués par un ciment organique (GRUET *et al.*, 1987) au niveau de l'organe constructeur. Cet organe grossit au cours de la croissance de l'animal, en même temps que le diamètre interne du tube ainsi que la taille des grains de sable utilisés (GRUET, 1984). Il en résulte des tubes plus ou moins flexueux, croissant verticalement en s'épaulant mutuellement. Cela donne naissance à des colonies parfois très importantes comme en baie du Mont-Saint-Michel (GRUET, 1986). Le tube arénacé de l'espèce *S. alveolata* est constitué pour l'essentiel de sables moyens (200 à 500 µm), moyennement classés, très bioclastiques (HOMMERIL, 1962 ; GRUET, 1982 ; VOVELLE, 1965).

La question posée ici est de vérifier expérimentalement si le choix de l'animal, lors du processus de construction, est influencé par la nature minéralogique, donc chimique, et surtout la forme des grains de sable.

## MATÉRIEL ET MÉTHODES

PRÉPARATION DU MATÉRIEL ÉTUDIÉ. — Des blocs de *Sabellaria alveolata* vivantes sont récoltés au lieu-dit "les Roches de la Fosse", à Noirmoutier (Vendée, France) et rapportés rapidement au laboratoire. Les tubes sont délicatement séparés les uns des autres. Puis, ils sont cassés transversalement dans leur portion terminale, de manière à ne laisser qu'une longueur de 10 mm (minimum) à 21 mm (maximum). Seuls sont conservés les plus gros individus, non lésés au cours de cette manipulation. Chaque animal est alors disposé à plat dans un cristallisoir numéroté. Il est immergé dans 2 à 3 cm d' eau de mer de salinité identique (35 P.S.U.) à celle du lieu d'origine des vers. Cette eau contient de la nourriture à base d'une culture d'algues unicellulaires. La non production de fèces étant un indice de mauvais état de l'animal, ceux-ci seront alors éliminés et remplacés avant le début de l'expérimentation. L'eau contenant la nourriture est changée tous les jours après une mise à sec de 4 heures, simulant une marée basse, mais non en phase avec le cycle lunaire.

- Une expérience préliminaire (GRUET, 1982) permet d'apprécier l'effet de la température sur la vitesse de reconstruction. Trois lots de quinze individus chacun ont été testés aux températures constantes (salles climatisées) de 13 °C, 16 °C et 20 °C.

- Deux autres expériences ont été menées en 1988 et 1989, mais à la même période (mois de mars), dans le même local, les mêmes récipients et selon le même protocole expérimental. Toutefois les conditions de température n'étaient pas identiques : en 1988 (du 9 au 25 mars, soit 17 jours) la température de l'eau varie entre 12 °C et 16,5 °C ; en 1989 (du 11 au 25 mars, soit 14 jours) la température oscille entre 14,5 °C (minimum) et 18,5 °C (maximum) pour des mesures effectuées vers 11 heures du matin. Or la température est un facteur déterminant pour la vitesse de reconstruction comme nous le montrons (GRUET, 1982) en expérience préliminaire. Chaque expérience a porté, au départ, sur des lots de 20 individus en 1988 et de 15 en 1989. Les animaux morts en cours d'expérience sont enlevés et le nombre d'individus vivants est precisé dans les tableaux (Tableaux 1, 2).

LE SÉDIMENT MIS À LA DISPOSITION DES *SABELLARIA* (Tableau 3). — Les différents sédiments proposés aux hermelles sont constitués de grains d'une granulométrie comprise entre 500 et 710 µm, ce qui correspond aux valeurs modales des tailles de grains utilisés dans la nature par des *Sabellaria alveolata* adultes dont le diamètre antérieur du tube oscille entre 2,3 mm et 3,5 mm (GRUET, 1984). Les différents lots de sédiment, composés d'éléments de même taille, diffèrent en revanche par la forme et la nature de ceux-ci :

- en 1982 : l'expérience préliminaire a été menée avec le même sable pour tous les individus. Il est *a priori* très favorable car provenant de la désagrégation de tubes. Sa nature est essentiellement quartzeuse avec quelques fragments coquilliers.

- en 1988 : coquilles de moules (carbonate de calcium) cassées donnant des fragments allongés en aiguilles acérées (lot A') ; sable de Loire composé de grains de quartz arrondis (61 %), de feldspaths sub-arrondis à anguleux (23 %), de micas aplatis et tranchants (0,8 %), de fragments divers dont surtout des minéraux lourds (15 %) (lot B') ; enfin un mélange en proportions égales de fragments de moules et de sable de Loire (lot C') ;

- en 1989 : les mêmes sédiments qu'en 1988 (moules : lot A ; sable de Loire : lot B) ; mais aussi un sable composite (lot C) récolté sur la plage de Ploemeur (Morbihan) formé de quartz subarrondis (51 %), de feldspaths

Source : MNHN, Paris

subarrondis à anguleux (32 %), de micas aplatis et à bords relativement tranchants (16 %) et de bioclastes arrondis (1 %) ; un sable de plage de St-Gildas (L.-A.) (lot D) ; ce même sable mais "traité" (lot E) pour en arrondir les grains. Ce sable usé par une longue agitation dans l'eau reste très proche du précédent, mais les grains sont un peu plus arrondis et émoussés.

TABLEAU 1. — Expérience de mars 1988 (17 jours). Lots A', B' et C'. Longueurs moyennes des tubes reconstruits par les *Sabellaria* en présence de différents types de sédiments (500 à 710 µm) à différents jours de l'expérimentation. Le nombre est celui des individus de l'expérience. Toutes les dimensions sont en mm.

| | Jours | 2 | 4 | 7 | 11 | 14 | 17 | Longueur du tube au départ | Diamètre interne du tube |
|---|---|---|---|---|---|---|---|---|---|
| LOT A' | nombre | 20 | 20 | 18 | 18 | 16 | 11 | 20 | 20 |
| | moyenne | 0,3 | 0,8 | 1,3 | 1,4 | 1,6 | 1,6 | 16,8 | 2,9 |
| | écart-type | 0,6 | 0,9 | 1,1 | 1,1 | 1,2 | 1,1 | 2,2 | 0,4 |
| LOT B' | nombre | 20 | 20 | 19 | 19 | 16 | 15 | 20 | 20 |
| | moyenne | 3 | 4,3 | 7,5 | 8,7 | 12,2 | 12,9 | 18,1 | 3 |
| | écart-type | 2 | 2,6 | 3,5 | 4,2 | 6,2 | 6,8 | 2,9 | 0,3 |
| LOT C' | nombre | 20 | 20 | 20 | 20 | 17 | 17 | 20 | 20 |
| | moyenne | 2,5 | 3,6 | 4,9 | 5,5 | 6,1 | 6,9 | 19,1 | 3,3 |
| | écart-type | 1,9 | 2,3 | 2,7 | 3 | 3,8 | 4 | 2,7 | 0,4 |

MODE OPÉRATOIRE ET MESURES. — Dans chaque cristallisoir, devant l'ouverture de chaque tube, est disposée une quantité identique de sédiment. L'animal reconstruit son tube en utilisant des grains mis à sa disposition. Du sédiment est régulièrement remis devant l'animal de telle façon qu'il n'en manque jamais. La portion de tube reconstruite, nettement visible, est mesurée périodiquement. Cela permet d'établir une courbe des longueurs de tube reconstruit en fonction du temps écoulé. Ces courbes obtenues dans les mêmes conditions seront donc comparables entre elles en fonction de la température pour l'expérience de 1979, en fonction du type de sédiment pour celles de 1988 et 1989.

Les valeurs moyennes obtenues ont été comparées entre elles par le test H de Kruskall et Wallis (SCHWARTZ, 1963), test non paramétrique adapté au faible nombre de valeurs.

En fin d'expérience, nous procédons au comptage des grains de diverses natures utilisés par l'animal le long de l'axe longitudinal du tube reconstruit, c'est-à-dire entre le début et la fin de l'expérience. Cela permet d'établir s'il y a eu, ou non, choix par l'animal d'un certain type de grain.

LES CONDITIONS NÉCESSAIRES A LA RECONSTRUCTION. — La méthode est celle employée par VOVELLE (1965) qui a montré la nécessité d'un reste de tube, le caractère artificiel et "anormal" du tube reconstitué, mais "n'en ayant pas moins une valeur fonctionnelle dans la mesure où il réalise une protection, déjà efficace au bout de 48 heures" (VOVELLE, 1965, p. 68). Le fondement de cette méthode tient au fait qu'un animal isolé dont on a cassé le tube tend rapidement à le reconstruire, à condition qu'il ait du sédiment "convenable" à sa portée. La vitesse de reconstruction dépend notamment de la température de l'eau. Celle-ci doit être supérieure à 4 °C pour avoir une reconstruction mesurable (GRUET, 1982).

L'expérience préliminaire de 1982 montre (voir plus loin) que l'on a intérêt à se situer entre 16 °C et 20 °C pour que cette vitesse soit nettement mesurable. Les conditions de l'expérience de 1989 s'en approchent. Pour l'année 1988 elles sont *a priori* moins favorables.

Enfin, la vitesse de reconstruction ralentit nettement au bout d'une quinzaine de jours, l'animal ayant reconstruit son "espace vital tubulaire". Continuer alors l'expérimentation n'apporte rien de plus. D'autre part, il n'est pas exclu que la taille du morceau de tube en début d'expérience, mais également l'âge de l'animal soient aussi des facteurs influant sur la vitesse de reconstruction. C'est pour cela que nous nous sommes situés dans un intervalle de taille moyenne de 16,8 mm à 21,1 mm pour la longueur de tube de départ, et un diamètre antérieur du tube variant entre 2,6 et 3,3 mm, c'est-à-dire que nous avons écarté les individus jeunes ou âgés (GRUET, 1982). Dans ces expérimentations, pour une même température, les différences de vitesses de reconstruction indiqueront donc une plus ou moins grande capacité à utiliser un certain type de sédiment caractérisé par la forme de ses grains.

Source : MNHN, Paris

TABLEAU 2. — Expérimentation de mars 1989 (14 jours). Lots A, B, C, D et E. Longueurs moyennes des tubes reconstruits par les *Sabellaria* en présence de différents types de sédiments (500 à 710 µm) à différents jours de l'expérimentation. Le nombre est celui des individus de l'expérience. Toutes les dimensions sont en mm.

| | Jours | 2 | 4 | 6 | 9 | 12 | 14 | Longueur du tube au départ | Diamètre interne du tube |
|---|---|---|---|---|---|---|---|---|---|
| LOT A | nombre | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 |
| | moyenne | 0,85 | 1,4 | 1,6 | 2,5 | 3,3 | 4,0 | 18,5 | 2,8 |
| | écart type | 1,2 | 1,6 | 1,6 | 1,7 | 1,7 | 2,0 | 3,2 | 0,4 |
| LOT B | nombre | 15 | 15 | 15 | 15 | 15 | 15 | 15 | 15 |
| | moyenne | 4,6 | 10,0 | 13,0 | 16,0 | 18,9 | 22,2 | 19,4 | 3 |
| | écart-type | 3,4 | 5 | 6 | 7,2 | 7,7 | 8,8 | 2,9 | 0,4 |
| LOT C | nombre | 15 | 15 | 15 | 15 | 15 | 15 | 15 | 15 |
| | moyenne | 8,1 | 12,6 | 19,1 | 24,6 | 29,2 | 34,7 | 21,1 | 2,6 |
| | écart-type | 3,4 | 5,9 | 7,2 | 9,4 | 11,4 | 13,7 | 4,8 | 0,5 |
| LOT D | nombre | 15 | 15 | 14 | 14 | 14 | 14 | 15 | 15 |
| | moyenne | 6,6 | 11,0 | 16,0 | 16,0 | 19,0 | 21,0 | 19,7 | 2,7 |
| | écart-type | 4,5 | 5,7 | 5,9 | 8,3 | 8 | 8,2 | 4,8 | 0,6 |
| LOT E | nombre | 15 | 15 | 15 | 15 | 14 | 12 | 15 | 15 |
| | moyenne | 5,7 | 10,3 | 13,6 | 16,4 | 18,1 | 22,0 | 18,9 | 2,8 |
| | écart-type | 4,2 | 5,0 | 7,0 | 9,7 | 10,6 | 12,0 | 4,2 | 0,8 |

## RÉSULTATS

Les courbes de reconstruction ont, pour la plupart, une allure générale qui permet de les diviser en trois portions : d'abord une phase de construction rapide (environ les sept premiers jours), puis une phase de ralentissement, se terminant par un palier. Les valeurs moyennes en fin d'expérience donnent une idée sur la vitesse de reconstruction.

TABLEAU 3. — Nature des grains du tube reconstruit des *Sabellaria* des lots B' et C' (Expérience de 1988); des lots B et C (expérience de 1989). Pourcentages de grains du sédiment de départ (D) et de celui du tube reconstruit (R).

| | 1988 | | | | 1989 | | | |
|---|---|---|---|---|---|---|---|---|
| | lot B' | | lot C' | | lot B | | lot C | |
| | D | R | D | R | D | R | D | R |
| Nombres de grains examinés | 119 | 873 | 119 | 850 | 119 | 823 | 120 | 1581 |
| moules brisées | - | - | 50% | 1.2% | - | - | - | - |
| bioclaste | - | - | - | - | - | - | 1 % | 2 % |
| quartz | 61,3 % | 80,5 % | 30,6 % | 80,8 % | 61,3 % | 81,9 % | 51 % | 68 % |
| feldspath | 22,7 % | 15,3% | 11,3 % | 11,4 % | 22,7 % | 14,5 % | 32 % | 29 % |
| mica | 0,8 % | 0 % | 0,4 % | 0 % | 0,8 % | 0% | 16 % | 0.5 % |
| "divers" | 15,1 % | 4,1 % | 7,5 % | 6,6 % | 15,1 % | 3,6 % | - | - |

EXPÉRIENCE PRÉLIMINAIRE : ACTION DE LA TEMPÉRATURE (GRUET, 1982). — Trois lots de 15 individus chacun ont été testés aux températures constantes (salles climatisées) de 13 °C, 16 °C et 20 °C. Les réponses individuelles sont très hétérogènes. Mais malgré cette forte variabilité le test de Kruskall et Wallis montre que les effets des températures sont significativement différents sur la reconstruction du tube (95 % de confiance). La signification est forte entre le deuxième et le neuvième jour. Les valeurs moyennes maximales du tube reconstruit en 13 jours avoisinent 25 mm à 20 °C, 20 mm à 16 °C et 7,5 mm à 13 °C. La vitesse maximale a été observée à 20 °C : 13 mm le premier jour, puis 6,7 mm par jour avant d'atteindre le palier de la courbe.

Source : MNHN, Paris

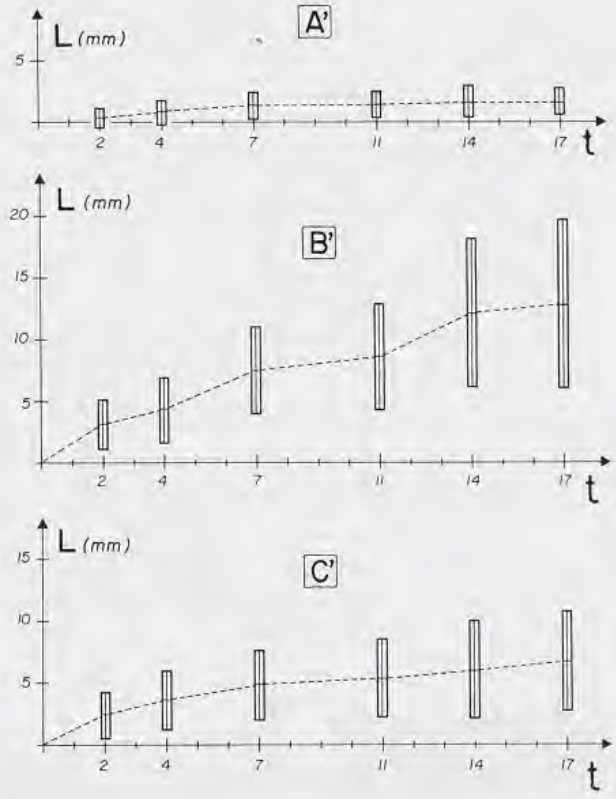



FIG. 1. — Vitesses de reconstruction (valeurs moyennes et déviations standards) des tubes au cours de l'expérimentation de mars 1988. L : longueur du tube reconstruit, en mm ; t : temps de reconstruction, en jours.

EXPÉRIMENTATION DE MARS 1988 : INFLUENCE DU TYPE DE SÉDIMENT (Tableau 1, Fig.1). — Lot A'. Dans les conditions de l'expérience, les longueurs du tube reconstruit par les *Sabellaria* à l'aide d'un sédiment composé exclusivement de coquilles de moules broyées (lot A) sont extrêmement réduites. Au bout de 17 jours, la moyenne des portions de tubes reconstruits n'atteint que 1,6 mm et dès le 7ème jour la croissance est quasi nulle. La plupart des grains utilisés pour la reconstruction sont en fait tombés de l'ancien tube lors des manipulations et réutilisés par l'animal.

Lot B'. Dans les mêmes conditions, mais en présence d'un sable de rivière (Loire) constitué de grains de quartz, de feldspath, de mica et de "divers" (lot B'), la reconstruction du tube est très nettement plus rapide (huit fois plus que pour le lot A') avec une moyenne de 12,9 mm au bout du même intervalle de temps. Le ralentissement de la croissance à partir du 7ème jour est à peine sensible. Les pourcentages de grains utilisés (Tableau 3) montrent une nette préférence des vers pour les grains de quartz, une moindre capture des grains de feldspath, un refus des micas et des "divers".

Lot C'. Toujours en conditions identiques, mais en présence d'un mélange des deux sables précédents en quantités égales, le tube est reconstruit à une vitesse intermédiaire (qyatre fois plus rapide que pour le lot A' et 2 fois moins que pour le lot B') avec une moyenne de 6,9 mm au bout des 17 jours. L'analyse et le comptage des grains utilisés (Tableau 3) montre que l'animal refuse en général (de 50 % à 1,2 %) les moules cassées pour utiliser environ 80,8 % de grains de quartz (30,6 % au départ), 11,4 % de feldspath pour 11,3 % au départ soit une même proportion, 0 % de mica (0,4 % au départ), 6,6 % de "divers" (7,5 % au début).

Le test de Kruskall et Wallis appliqué à ces trois lots montre des différences significatives (95 % de confiance) entre le deuxième jour et le onzième jour ; puis du quatorzième jour (90 % de confiance) au 17ème (10 %) la signification diminue.

Source : MNHN, Paris

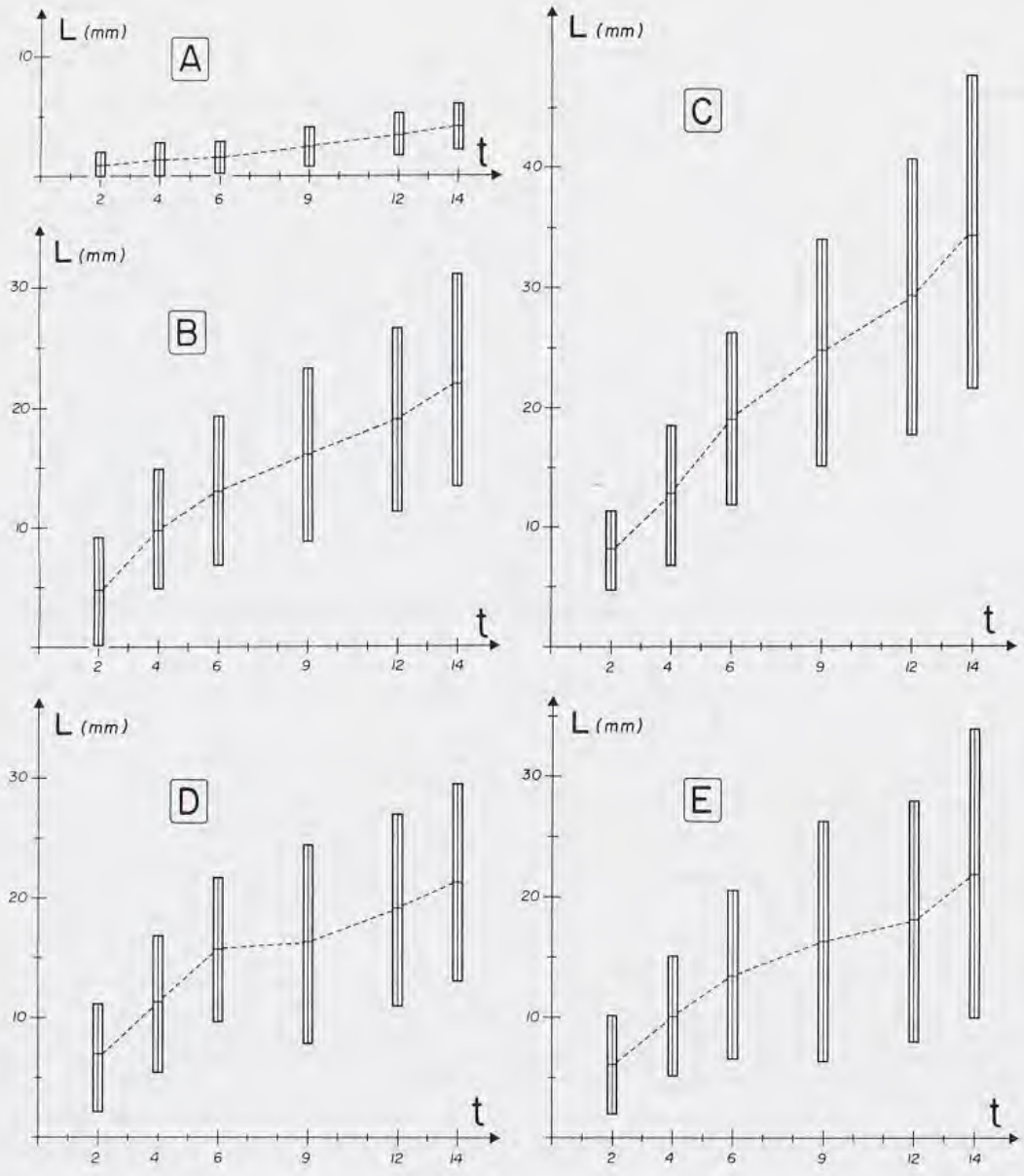



FIG. 2. — Vitesses de reconstruction (valeurs moyennes et déviations standards) des tubes au cours de l'expérimentation de 1989. L : longueur du tube reconstruit, en mm ; t : temps de reconstruction, en jours.

EXPÉRIMENTATION DE MARS 1989 : INFLUENCE DU TYPE DE SÉDIMENT (Tableau 2, Fig. 2). — Cette expérimentation répète partiellement celle de 1988 mais en la complétant avec d'autres types de sédiments.

Lots A et B. Les résultats (valeurs moyennes) pour ces deux premiers lots, constitués exactement des même sables qu'en 1988, sont tout à fait semblables à ceux de 1988. Seules les valeurs absolues diffèrent légèrement. Elles sont plus élevées en 1989 (2,5 fois plus pour le lot A et 1,7 fois pour le lot B), ce qui peut s'expliquer simplement par la température de l'eau, plus forte en 1989. Les conclusions concernant la nature du sédiment sont similaires : il y a un très net refus des moules brisées et des micas, une préférence pour les quartz et un peu moins pour les feldspaths.

Lot C (Tableau 2, Fig. 2). Il est constitué d'un sable de plage marine composé d'un mélange de quartz (51 %), de feldspath (32 %), de mica (16%) et de bioclastes (1 %). La reconstruction du tube est la plus rapide que nous

Source : MNHN, Paris

ayons obtenue, 1,6 fois plus élevée que pour le lot B. Il y a bien un ralentissement au bout de 7 jours mais le palier ne paraît pas encore atteint en fin d'expérience au bout de 14 jours. Les grains de quartz et les bioclastes sont préférentiellement choisis, les feldspaths un peu moins. Par contre les micas sont nettement "repoussés" (de 16 à 0,5 %) ainsi que les "divers".

Lots D et E (Tableau 2, Fig. 2). Ces expériences complémentaires réalisées à partir d'un sable de haute plage riche en grains de quartz et en bioclastes, mais aussi en feldspaths et micas, donnent une vitesse de reconstruction pratiquement identique à celle du lot B (sable de la Loire). Elles confortent l'ensemble des résultats précédents.

Le test de Kruskall et Wallis appliqué à ces courbes permet de dire que la signification statistique diminue du 2ème jour (98% de confiance), au 4ème (5 à 10 %), au 6ème (10 à 20 %), au 9ème (20 %), au 12ème (20 à 30 %), au 14ème (30 à 50 %). Ce test n'autorise pas à dire que les conclusions avancées sont fausses, mais qu'elles ne sont pas statistiquement valables si l'on retient le seuil de 95 % de confiance. Cela tient à la forte variabilité individuelle qu'il aurait fallu compenser par un beaucoup plus grand nombre d'individus ce qui est difficilement réalisable pour des raisons pratiques.

## DISCUSSION ET CONCLUSIONS

Après ces expérimentations menées en laboratoire, nous pouvons dire que la nature minéralogique, donc chimique, des grains de sable utilisés par *Sabellaria alveolata* ne semble pas jouer de rôle décisif dans le choix des

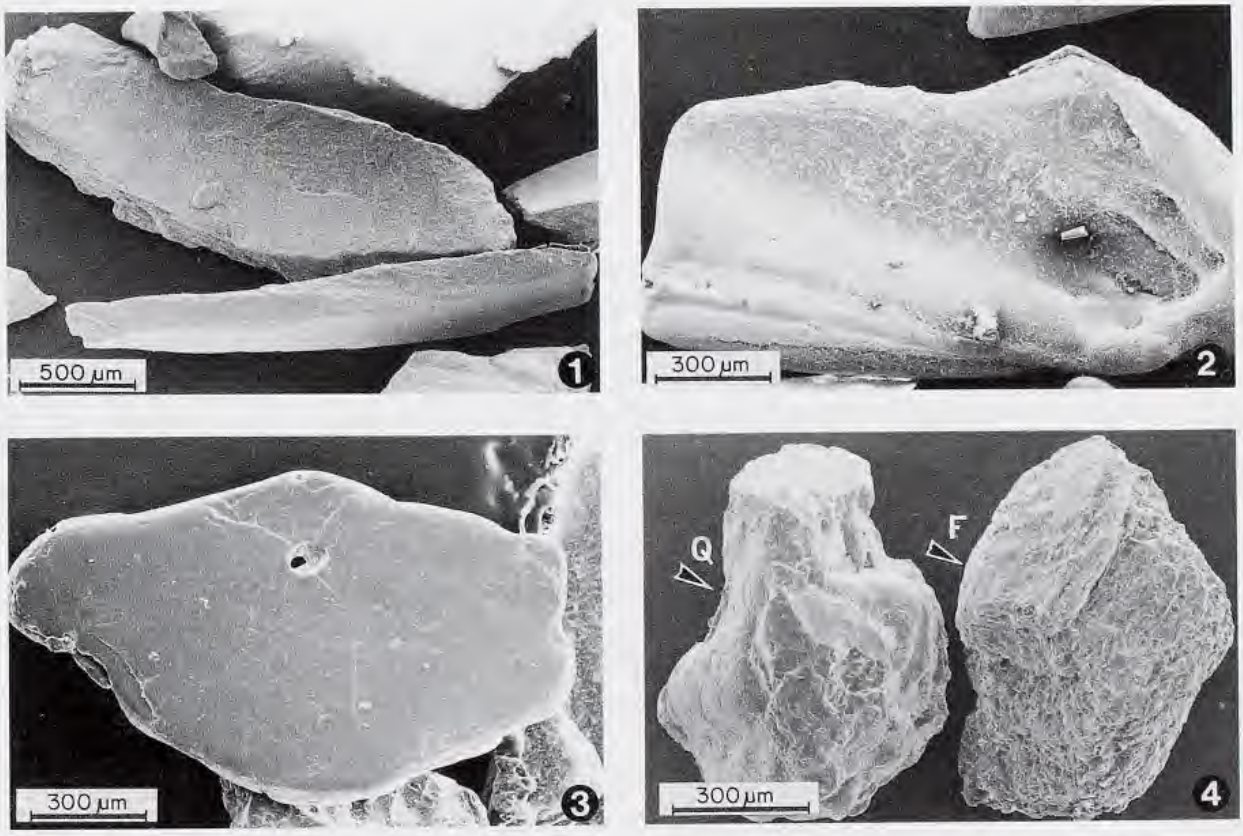



FIG. 3. — Grains de différentes natures et morphologies ayant été utilisés au cours des expérimentations. 1 : moule brisée ; 2 : bioclaste ; 3 : mica ; 4 : quartz (Q) et feldspath (F).

Source : MNHN, Paris

grains de sable par celui-ci. La morphologie des grains, par contre, semble être un facteur déterminant pour une même granulométrie du sédiment. En effet :

- les moules brisées artificiellement (lot A' de 1988) correspondent aux vitesses de croissance les plus faibles et sont pourtant constituées de carbonate de calcium, de même que les bioclastes qui sont eux associés à des croissances rapides (lots C, D et E de 1989). La seule différence vient de la morphologie de ces éléments, très anguleux et en aiguilles dans le premier cas, bien arrondis dans le second cas (Fig. 3, photos 1 et 2).

- les proportions de quartz utilisés sont toujours supérieures à celles de départ et le quartz est un peu plus employé que le feldspath. Ce choix relatif entre quartz et feldspath est peut-être à mettre en relation avec la micromorphologie légèrement plus lisse des quartz (Fig. 3, photo 4), plutôt que de l'attribuer à de subtiles différences chimiques entre ces minéraux tous deux silicatés.

- le très net rejet des grains de micas, plats et à bords tranchants (Fig. 3, photo. 3), corrobore l'hypothèse du point précédent, les micas étant eux aussi des minéraux silicatés, chimiquement proches des feldspaths.

- on pourrait enfin se poser la question d'une éventuelle influence "de type catalyseur" des mélanges de grains, par rapport aux sédiments mono-minéraux ?

On a déjà montré (GRUET, 1984) que ces Annélides Polychètes choisissent la taille des grains de sédiment, et celà en relation avec les dimensions de l'organe constructeur par où chaque grain passe pour être englué de ciment avant d'être collé sur le tube. Les *Sabellaria* ont-elles, aussi, la capacité d'estimer la géométrie des matériaux mis à leur disposition ? Ces expérimentations le démontrent. Le refus de grains de formes anguleuses, allongées ou aplatis peut se réaliser à plusieurs niveaux du mécanisme constructeur décrit par VOVELLE (1965) : au moment où le filament oral capte le grain, plus tard lors de son cheminement le long des gouttières ciliées et enfin au niveau de l'organe constructeur en fer à cheval.

## REMERCIEMENTS

Nous exprimons nos remerciements à M. le Professeur J. VOVELLE qui nous a toujours encouragés dans nos recherches et qui a relu notre manuscrit, à M.A. COSSARD (Laboratoire de Géologie, Université de Nantes) et à M.G. HAURAY qui ont contribué à l'élaboration du "poster" auquel correspond cet article.

## RÉFÉRENCES

GRUET, Y., 1982. — *Recherches sur l'écologie des "récifs" d'hermelles édifiés par l'Annélide Polychète* Sabellaria alveolata *(Linné)*. Thèse de Doctorat d'Etat ès Sciences, Univ. Nantes, 234 pp.

GRUET, Y., 1984. — Granulometric evolution of the sand tube in relation to growth of the Polychaete Annelid *Sabellaria alveolata* (Linné) (Sabellariidae). *Ophelia*, **23** : 181-193.

GRUET, Y., 1986. — Spatio-temporal changes of sabellarian reefs built by the sedentary Polychaete *Sabellaria alveolata* (Linné). *Marine Ecology*, **7** : 303-319.

GRUET, Y., VOVELLE, J. & GRASSET, M., 1987. — Composante biominérale du ciment du tube chez *Sabellaria alveolata* (L.), Annélide Polychète. *Can. J. Zool.*, **65** : 837-842.

HOMMERIL, P., 1962. — Étude locale (Gouville-sur-mer, Manche) de la retenue des sédiments par deux Polychètes sédentaires: *Sabellaria alveolata* (Hermelle) et *Lanice conchilega*. *Cah. océanogr.*, **15**ème année (4) : 245-257.

ORRHAGE, L., 1978. — On the structure and evolution of the anterior end of the Sabellariidae (Polychaeta, Sedentaria). With some remarks on the general organisation of the polychaete brain. *Zool. Jahrb. Abt. Anat.*, **100** : 343-374.

SCHWARTZ, D., 1963. — *Méthodes statistiques à l'usage des médecins et des biologistes*. Éditions Flammarion, Paris, 358pp.

VOVELLE, J., 1965. — Le tube de *Sabellaria alveolata* (L.) Annélide Polychète Hermellidae et son ciment. Étude écologique, expérimentale, histologique et histochimique. *Arch. Zool. exp. gén.*, **106** : 1-187.

Source : MNHN, Paris

# Les vers polychètes et l'estuaire de la Loire au début du 20ème siècle par G. FERRONIÈRE (1875-1922)

*Yves GRUET, Jocelyne MARCHAND & J. BAUDET*

Laboratoire de Biologie Marine, 2, rue de la Houssinière
44072 Nantes Cedex 03, France

RÉSUMÉ

G. FERRONIÈRE, architecte de profession, réalisa des études de géologie et de biologie marine ; il fut l'un des pionniers de l'écologie expérimentale. Ses travaux de systématique (Oligochètes et Polychètes) lui ont conféré une réputation internationale. Ses études de faunistique, notamment sa cartographie biologique de l'estuaire de la Loire (1901), constituent des documents de référence pour en estimer l'évolution temporelle. Ainsi, en 90 ans, les espèces euryhalines ont progressé vers l'amont de l'estuaire : *Boccardiella ligerica* de 22 km et *Nereis diversicolor* de 11 km. Par contre, l'espèce stenohaline *Arenicola marina* conserve la même distribution spatiale.

ABSTRACT

**The polychaete worms and the estuary of the river Loire at the beginning of the 20th century by G. FERRONIÈRE (1875-1922)**

G. FERRONIÈRE was an architect by profession but also a scientist. He published results in the fields of geology and biology and was one of the pioneers of ecology. He remains well-known for his works of taxonomy oligochaetes and polychaetes. The biological changes in the estuary of the Loire can be estimated since his studies on the distribution patterns of benthic species (1901). In 90 years, the euryhaline species have moved up-stream in the the estuary: 22 km for *Boccardiella ligerica* and 11 km for *Nereis diversicolor* from the previous point. On the contrary, the pattern distribution of the stenohaline worm *Arenicola marina* remains as it was.

## INTRODUCTION

Georges FERRONIÈRE est né le 5 juin 1875 à Nantes. Sa famille paternelle vivait du négoce tandis que celle de sa mère comportait plusieurs architectes. Il restera fidèle à cette tradition familiale en devenant lui aussi architecte. Son enfance passée dans le port de Nantes lui donne probablement le goût de la mer. En outre, durant les vacances, il descend la Loire en bateau pour passer une partie de l'été sur la côte du Croisic. Brillant élève, il devient bachelier ès-Sciences à dix sept ans. A l'Université Catholique d'Angers, il prépare et obtient la Licence ès-Sciences naturelles. Dès cette époque il fréquente d'illustres naturalistes et participe à la vie de Sociétés

GRUET Y., MARCHAND , J. & J. BAUDET , 1994. — Les vers polychètes et l'estuaire de la lLire au début du 20ème siecle par G. FERRONIÈRE (1875-1922). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 433-439. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

Scientifiques et de Musées. Ses relations amicales avec le Dr. Louis BUREAU, Directeur du Muséum de Nantes, lui permettent de connaître Edouard BUREAU, Professeur de Géologie au Muséum national d'Histoire naturelle de Paris qui l'aide à acquérir des compétences dans cette discipline. Parallèlement, il prépare à l'Ecole des Beaux Arts à Paris son diplôme d'architecte. En plus de ses activités professionnelles, il prépare, de 1897 à 1901, une thèse de Biologie à la Sorbonne à Paris. Il choisit un sujet de biologie marine, auquel il peut se consacrer dans le petit laboratoire qu'il s'est aménagé dans la villa familiale sur la côte battue du Croisic, à proximité de l'estuaire de la Loire et des marais salants. En 1901 il présente son mémoire intitulé : "Etudes biologiques sur la faune supralittorale de la Loire Inférieure". Son deuxième sujet de thèse comportait une étude de botanique et une étude de Géologie. Ce travail d'écologie fut jugé avec mention "Très Honorable", par Yves DELAGE, biologiste marin, Gaston BONNIER, célèbre botaniste et MUNIER-CHALMAS, géologue. En 1901, il épouse Augustine GOUIN ; ils auront sept enfants. Il consacre son énergie à sa profession d'architecte, à ses recherches en biologie et géologie ainsi qu'à plusieurs charges d'enseignement. Ainsi, il a assuré des cours de géologie à l'Ecole Supérieure d'Agriculture d'Angers ; il fut aussi Chargé d'enseignement de l'Histoire de l'Art à la Faculté des Lettres d'Angers et même d'un cours sur les "marchandises" ou "matières commercialisables" à l'Ecole Supérieure de Commerce de cette même ville. La variété de ces charges illustre la diversité des compétences de ce travailleur qui devait partager son temps entre Nantes, Angers et Paris. Ses qualités pédagogiques sont confirmées par les nombreuses conférences pour lesquelles il était sollicité. Il participa activement à la vie des Sociétés Scientifiques locales (BAUDET *et al.*, 1991). Il fut membre et parfois fondateur de Sociétés de Sciences Naturelles, de Géologie, d'Archéologie, d'Océanographie. Il a aussi oeuvré à la création et à l'extension de collections comme celles du Musée lapidaire de Nantes dont il fut conservateur. Il mourut subitement, à 47 ans, laissant inachevés certains travaux. C'est son ami Joseph PÉNEAU, qui prit soin de réunir ses publications et notes scientifiques et qui rédigea sa notice nécrologique. Nous présentons son activité de biologiste se rapportant aux travaux d'inventaires, d'expérimentations, de morphologie et de systématique d'Annélides.

## LES TRAVAUX D'INVENTAIRE

La thèse de G. FERRONIÈRE comporte une première partie intitulée " Etude de divers faciès de la zone supralittorale. Distribution des vers supralittoraux" avec quatre chapitres : -I- zone supralittorale dans les eaux vives ; -II- "Le traict" du Croisic ; -III- Marais salants ; -IV- Eaux saumâtres et douces. Les résultats de ses nombreuses excursions dans des milieux aussi diversifiés lui ont permis d'inventorier et cartographier de très nombreuses espèces. L'auteur s'était particulièrement attaché à leur distribution spatiale selon les gradients halins : de l'eau douce de la Loire jusqu'aux eaux marines puis de l'eau de mer jusqu'aux eaux sursalées des marais salants. Il avait relevé le fait que certaines formes aquatiques habitent aussi bien les eaux sursalées que dessalées et qu'elles sont très résistantes. Il avait également abordé la notion, particulièrement importante en estuaire, de la distribution verticale des espèces, liée à la stratification des eaux en fonction de leur salinité. Nous retiendrons sa cartographie des espèces (supralittorales) caractéristiques de la Basse Loire. Ce travail est en effet indispensable pour apprécier les changements biologiques qui sont intervenus pendant le 20ème siècle (Fig. 1). Depuis le 19ème siècle, l'estuaire de la Loire a connu de vastes travaux d'amènagement qui ont profondément modifié sa morphologie, sa bathymétrie et son hydrologie.

Dans le secteur aval (Donges), le chenal de navigation a été creusé de 4,25 m entre 1953 et 1976, puis de 3,25 m. Par ailleurs, depuis 1945, des centaines d'hectares de zones humides ont été remblayées et endiguées pour l'implantation de zones industrielles. De ce fait le linéaire de berges naturelles est passé de 300 km à 50 km et l'envasement des estrans s'est accéléré. D'un point de vue hydrosédimentaire, ces aménagements ont eu pour conséquence de provoquer la remontée de la marée dynamique de 30 km en 75 ans, celle du front de salinité (0,5 P.S.U.) de 20 km et celle du bouchon vaseux de 10 km avec un doublement du volume des matières en suspension (environ 700 000 tonnes). Depuis le début du siècle, les changements hydrosédimentaires ont entraîné la progression vers l'amont des limites de distribution d'un certain nombre d'espèces benthiques estuariennes, comparativement à ce qu'avait cartographié FERRONNIÈRE. Ainsi, depuis 1901, *Nereis diversicolor* a progressé d'environ 11 km et *Boccardiella ligerica* de 22 km, tandis que les limites de distribution d'*Arenicola marina* n'ont pratiquement pas évolué (MARCHAND, 1972). Par ailleurs, les espèces à cycle court comme *Boccardiella ligerica* peuvent s'implanter temporairement bien en amont de leurs limites habituelles lors des années de grande sécheresse. Il est certain que le surcreusement du chenal de l'estuaire et la destruction de nombreuses zones humides ont eu pour conséquence la perte d'une grande partie des potentialités biologiques de cet écosystème, notamment de ses potentialités nourricières.

Source : MNHN, Paris

TABLEAU 1. — Évolution des distributions spatiales de trois espèces de polychètes dans l'estuaire de la Loire, depuis 1901.

| | | Saint-Nazaire 0 km | Méan 2 km | Donges 10 km | Lavau 18 km | Cordemais 26 km | Couëron 38 km |
|---|---|---|---|---|---|---|---|
| *Arenicola marina* | 1901 | + | - | - | - | - | - |
| | 1980 | + | - | - | - | - | - |
| *Boccardiella ligerica* | 1901 | + | + | + | + | - | - |
| | 1980 | + | + | + | + | + | + |
| *Hediste (Nereis) diversicolor* | 1901 | + | + | + | + | - | - |
| | 1980 | + | + | + | + | + | + |

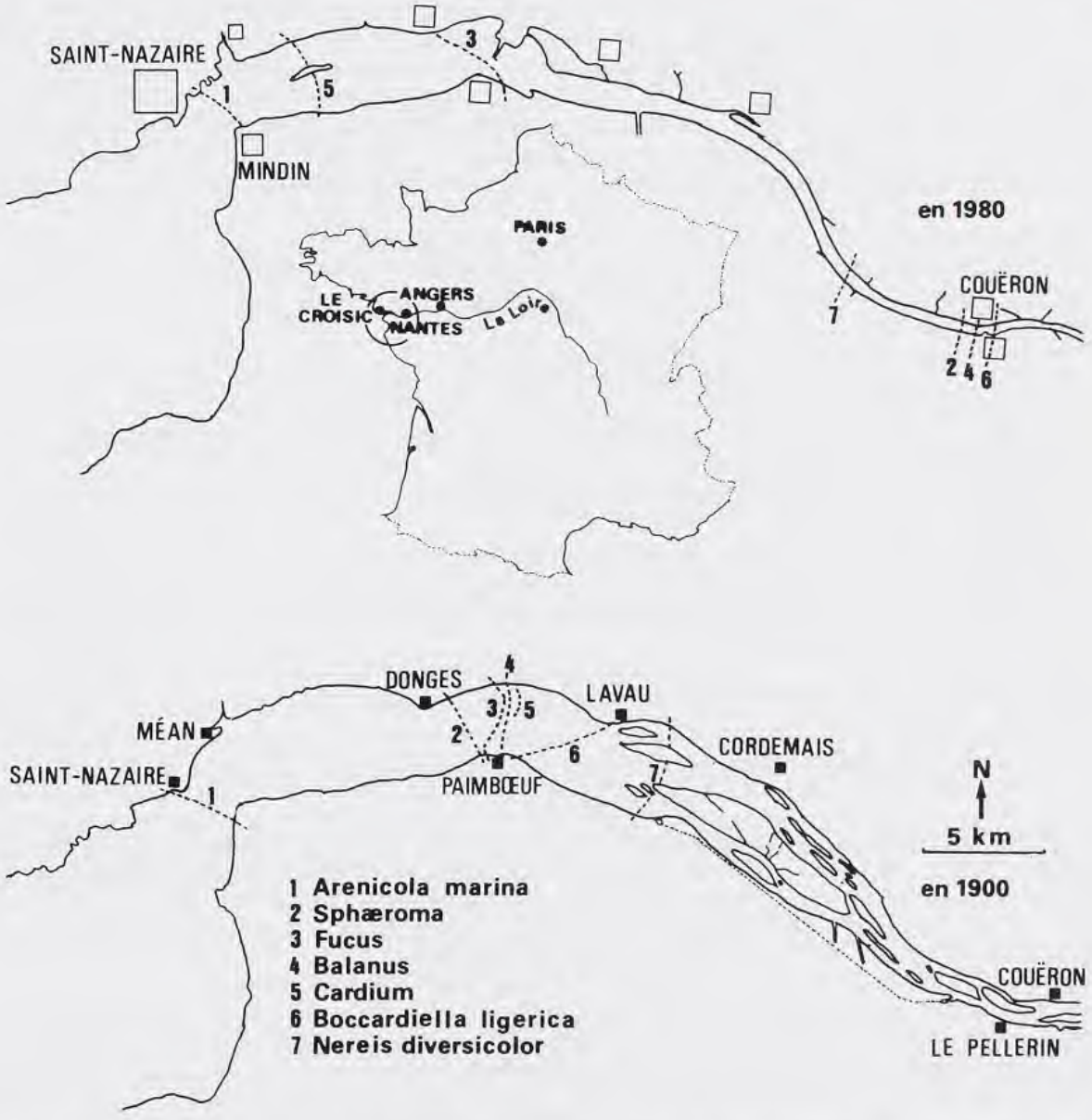



FIG. 1. — Carte de France situant les lieux de travail de Georges FERRONIÈRE et cartes comparant la distribution de quelques espèces en 1900 d'après FERRONNIÈRE et en 1980 d'après MARCHAND.

Source : MNHN, Paris

## LES EXPÉRIMENTATIONS

G. FERRONIÈRE voulait démontrer que la répartition des espèces intertidales dépend des facteurs du milieu et de leurs variations : "*Il nous reste maintenant à reproduire expérimentalement ces changements de milieux et à étudier les conséquences qui en découlent pour chaque espèce.*". Pour prouver que certaines espèces sont adaptées aux changements cycliques de conditions (marées, cycles de marées, saisons) et qu'elles ont été sélectionnées par les contraintes environnementales, il a expérimenté dans quatre domaines. La seconde partie de sa thèse : "Etude expérimentale de quelques conditions de milieu agissant sur les animaux supralittoraux" comporte quatre chapitres principaux traitant de : I- la dessication ; II- le passage de l'eau de mer à l'eau douce ; III- le passage de l'eau de mer à l'eau sursalée ; IV- l'influence de la lumière. Ces thèmes se prêtaient à une expérimentation simple, réalisable dans son petit laboratoire et caractérisaient bien la zone des marées (dessication, variation de la lumière) et le gradient halin croissant de l'estuaire de la Loire, à la mer, jusqu'aux marais salants. De nombreux groupes de vers marins, dulçaquicoles et même terrestres ont été testés : Planaires, Némertes, Oligochètes et surtout Polychètes. Pour ce dernier groupe, l'expérimentateur récoltait sur l'estran des animaux frais, tenait compte de leur taille, de leur état de maturité et même de leur provenance sur les différents niveaux de l'estran. L'expression des résultats était aussi simple que l'évaluation des paramètres ; l'auteur décrivait la réaction des animaux aux stimuli, dessinait éventuellement leurs déplacements. La plupart du temps la résistance des vers aux changements de conditions est exprimée en temps de survie. Grace à ses expérimentations qui ne faisaient varier qu'un seul facteur environnemental à la fois, il pouvait apprécier la tolérance des espèces. La richesse faunistique de la côte du Croisic a permis à G. FERRONIÈRE de tester plus de cinquante espèces de Polychètes parmi lesquelles nous avons noté :

- Syllidae : *Syllis alternosetosa* ; *S. gracilis* ; *S. prolifera*; *S. vivipara* ;
- Phyllodocidae : *Eulalia viridis* ; *E. quadrilineata* ; *E. rubiginosa* ; *Phyllodoce bilineata* ; *P. laminosa* ;
- Aphroditidae : *Sthenelais idunae* ; *Lepidonotus clava* ; *L. squamatus* ; *Lagisca extenuata* ; *Halosydna gelatinosa* ; *Eteone picta* ;
- Eunicidae : *Lysidice ninetta* ; *Marphysa sanguinea* ; *M. bellii* ;
- Nereidae : *Nereis longipes* ; *N. cultrifera* (y compris la forme *Heteronereis*) ; *N. pelagica* ; *Hediste (Nereis) diversicolor* ; *N. dumerili* ; *N. irrorata* ;
- Spionidae : *Boccardia ligerica* ; *B. polybranchiata* ; *Malacoceros vulgaris* ; *Polydora ciliata* ; *P. caeca* ;
- Sabellidae : *Fabricia sabella* ;
- Cirratulidae : *Dodecaceria concharum* ; *Audouinia tentaculata*; *Cirratulus filiformis* ;
- Capitellidae : *Capitella capitata* ;
- Chloraemidae : *Flabelligera affinis* ; *Stylarioides plumosus* ;
- Arenicolidae : *Arenicola marina* ; *A. grubei* ; *A. ecaudata* ;
- Terebellidae : *Polycirrus hematodes* ; *Terebella lapidaria* ; *Lanice conchylega* ;
- Serpulidae : *Pomatoceros triqueter* .

Dans ce travail G. FERRONIÈRE fait preuve d'une grande curiosité scientifique et se tient au courant des travaux de ses contemporains (chaque chapitre est introduit par un "état de la question").

## TRAVAUX EN MORPHOLOGIE ET SYSTÉMATIQUE D'ANNÉLIDES

G. FERRONIÈRE avait tout d'abord entrepris des études sur les Oligochètes, s'appuyant sur une bibliographie mondiale complète. Travaillant sur la frange supérieure des estrans et sur des points d'eau douce temporaires, il étudia des espèces aux modes de vie sub-aquatiques. Les Oligochètes aquatiques (Aelosomatidés, Naididés, Tubificidés et Haplotaxidés) furent également abordés. Systématicien et faunisticien renommé pour les Oligochètes (BRINKHURST, 1963), il l'est également pour les Polychètes.

C'est dans la première de ses trois "*contributions à l'étude de la faune de la Loire-Inférieure*" qu'il reprend la description de deux espèces de *Protodrilus* (Archiannélides). Son nom reste attaché à *Boccardiella ligerica* (Spionidae), espèce nouvelle qu'il décrit en 1898. Jeune chercheur, il découvre cette espèce dans les vasières de la Basse Loire et la dédie à ce fleuve (*Liger* en latin). Ce ver "*habitait des tubes de vase, sous les pierres ou dans des fentes de rochers à demi envahis par la boue noire et fine qui forme, presque partout, le fond, dans cette partie de l'embouchure de la Loire*". Dans sa description, l'auteur s'attache aux détails qui différencient cette espèce de *Polydora ciliata* et de *Polydora* (*Boccardia*) *polybranchiata*. La publication illustrée permet d'identifier avec certitude l'espèce, mais le fait qu'il n'y ait apparemment pas eu dépôt de type ou de paratype peut, en partie,

Source : MNHN, Paris

expliquer les confusions et redescriptions que d'autres auteurs firent par la suite (Fig. 2). Ainsi, R. HORST décrit en 1920 *Polydora redeki* du Zuiderzee (Pays-Bas) et en 1927, P. FAUVEL, reconnaît l'existence de deux espèces différentes *P. ligerica* et *P. redeki* dans sa faune des "Polychètes Sédentaires". En 1960, F. RULLIER, à partir d'échantillons de Normandie (France), reprend la morphologie de *Polydora* (*Boccardia*) *redeki*, sans faire le rapprochement avec *B. ligerica* de la Loire. Ce n'est qu'en 1971 que BLAKE & WOODWICK réexaminent l'ensemble des échantillons et démontrent la synonymie entre *P. redeki* Horst, 1920 et *B. ligerica* Ferronnière, 1898. Selon la règle d'antériorité, la seconde dénomination est la seule valide. Avec la révision des genres de Spionidés, publiée par BLAKE & KUDENOV en 1978, apparaît *Boccardiella* gen. nov. auquel ces auteurs rattachent *Boccardia ligerica* qui désormais devient *Boccardiella ligerica* (Ferronnière, 1898)

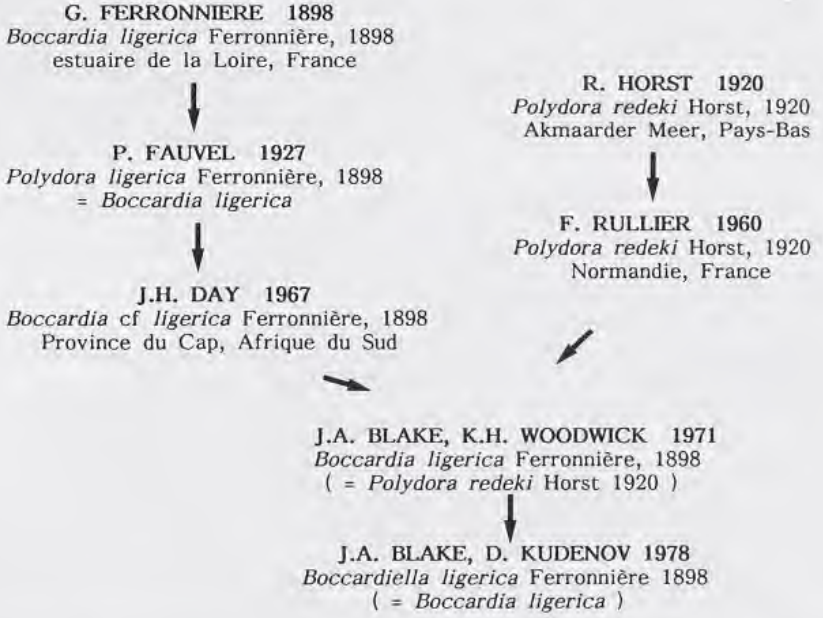



FIG. 2. — Schéma résumant l'histoire de la nomenclature du Ver Polychète Spionidé *Boccardia ligerica* Ferronnière, 1898, devenu *Boccardiella ligerica* (Ferronnière, 1898) en 1978 (BLAKE & KUDENOV, 1978).

Espèce suspensivore, ce ver serait favorisé par l'envasement. Il peut former des revêtements denses de tubes sur les blocs, au bas de l'estran (Fig. 3). D'après ROBINEAU, 1986, cette espèce d'eau saumâtre s'accomode de salinités variant de 18 à 0,5 P.S.U., avec un développement maximum entre 11 et 7,7 P.S.U.. Longtemps connue du seul estuaire de la Loire, *Boccardiella ligerica* présente actuellement une large distribution en zone tempérée, dans des stations envasées, souvent associée au Serpulidé *Ficopomatus enigmaticus* (Fauvel). On la trouve aux Etats-Unis (côte est), mais aussi en Afrique du Sud (DAY, 1967). Il est probable que les transports maritimes aient favorisé cette large répartition.

## CONCLUSION

Le sujet de thèse de G. FERRONIÈRE se situe tout à fait dans dans les idées "*modernes*" de la fin du 19ème siècle : le but est d'expliquer la distribution géographique des animaux, d'élucider les questions d'origine de la faune, de montrer comment les espèces s'acclimatent aux différents milieux... Le choix de l'estran a l'avantage de présenter une très grande diversité de faciès écologiquement bien différenciés. Par ailleurs, il a fait preuve d'innovation en abordant l'étude des zones sursalées des marais salants et les secteurs dessalés de l'estuaire de la Loire. La cartographie des espèces caractéristiques de la Basse-Loire, effectuée en 1901, reste une référence régionale et constitue un "état initial" essentiel pour apprécier l'évolution écologique de l'estuaire suite aux

Source : MNHN, Paris

FIG. 3. — Quelques aspects des populations de *Boccardiella ligerica* dans l'estuaire de la Loire. Certains blocs sont recouverts d'un tapis continu de tubes (Photo LE MAGUERESSE & GRUET).

profondes modifications physiques (chenalisation) qu'il a subies. Le chercheur G. FERRONIÈRE partagea son énergie et sa passion entre la biologie, la géologie et sa profession d'architecte. Son oeuvre scientifique n'en fut pas moins remarquable ; elle est toujours consultée et cet auteur reste reconnu , notamment en systématique, comme un "spécialiste" ; à ce titre, il figure toujours dans les bibliographies. Son nom restera lié à celui de l'espèce nouvelle qu'il découvrit en Loire.

## LISTE DES TRAVAUX DE G. FERRONNIÈRE EN BIOLOGIE

1898 a — 1ère contribution à l'Étude de la faune de la Loire-Inférieure (Polygordiens, Spionidien, Némertien). *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (3-4) : 101-115.

1898 b — Quelques vers récoltés au Croisic. Polychètes, Polygordiens, Némertiens. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (3-4), : XXI-XXIII.

Source : MNHN, Paris

1898 c — Quelques vers de Loire-Inférieure. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (3-4): 31-42.

1899 a — 2ème contribution à l'Étude de la faune de Loire-Inférieure (Pseudo-scorpions, Myriapodes, Annélides), *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (2) : 137-146.

1899 b — 3ème contribution à l'Étude de la faune de la Loire-Inférieure (Oligochètes littoraux et supralittoraux). *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (3) : 229-298.

1900 a — Sur *Gryllotalpa vulgaris*, courtilière variété foncée des Marais salants. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, : 15.

1900 b — Une Annélide intermédiaire entre les Spionidiens et les Cirrhatulidiens. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes : 16.

1901 a — Études biologiques sur la faune supralittorale de la Loire-Inférieure. Première thèse, Faculté des Sciences de Paris, Série A, n° 392, n° d'ordre : 1063, 453 pages. Imprimeur-Editeur R. Guist'hau, A. Dugas, Nantes.

1901 b — Études biologiques sur les zones supralittorales de la Loire-Inférieure. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (1-2) : 1-453.

1902 a — Sur un Phyllopode éclos à la Sorbonne dans des bocaux contenant de la boue provenant de la République Argentine. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (1-4) : 25.

1902 b — Sur *Aepophilus Bonnairei*, *Anurida maritima*, etc.. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (1-4) : 26.

1906 — Observation sur *Aepus Robini*. *Bull. Soc. Sc. nat. Ouest Fr., Nantes*, (1-4) : 34.

1907 — Envoi au Muséum de Nantes d'une Epinoche pêchée à la Bernerie. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (3-4) : 5.

1910 — A propos du travail du Dr Horst : De Anneliiden der Zuiderzee. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, (3-4) : 8.

## RÉFÉRENCES


BAUDET, J., GRUET, Y., LEBEL, A., MAILLARD, Y., MARCHAND, J., 1991. — Georges Henri Joseph FERRONNIÈRE. Son oeuvre en Biologie marine. *Bull. Soc. Sc. nat. Ouest Fr.*, Nantes, suppl. hors série : 50-75.

BLAKE, J.A. & KUDENOV,D.,1978. — The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. *Mem. Nat. Mus. Vic.*, **39** : 171-280.

BLAKE, J.A. & WOODWICK, K.H., 1971. — A review of the genus *Boccardia* Carazzi (Polychaeta: Spionidae) with descriptions of two new species. *Bull. So. Calf. Acad. Sci.*, **70** : 31-42.

BRINKHURST, R.O., 1963. — Taxonomical study on the Tubificidae (Annelida Oligochaeta). *Inst. Rev. Ges. Hydr.*, suppl., **2** : 1-83.

DAY, J.H., 1967. — *A Monograph on the Polychaeta of Southern Africa*. Part 2. Sedentaria. Trustees of the Brit. Mus. (Nat. Hist.), London, 878 pp.

FAUVEL, P., 1927. — *Polychètes Sédentaires*. Faune Fr. **16** : 1-494.

HORST, R., 1920. — Polychaete Anneliiden uit het Alkmaarder Meer door Dr. R. Horst. *Zool. Meded.*, Leiden, **5** : 110-111.

MARCHAND, J., 1972. — Bionomie benthique de l'estuaire de la Loire I. Observations sur l'estran maritime de la mer à Cordemais. *Rev. Trav. Inst. Pêches marit.*, **36** : 47-67.

ROBINEAU, B., 1986. — *Les peuplements benthiques dans l'estuaire de la Loire*. Thèse de Doctorat, Université de Bretagne occidentale, 330 pp.

RULLIER, F., 1960. — Morphologie et développement du Spionidae (Annélide : Polychète) *Polydora (Boccardia) redeki* Horst. *Cah. Biol. mar.*, **1** : 231-244.


Source : MNHN, Paris

Source : MNHN, Paris

# Temporal and spatial patterns in the distribution of infaunal Polychaetes in Jervis Bay, New South Wales, Australia

*Patricia A. HUTCHINGS* & Charles A. JACOBY***

* The Australian Museum, P.O. Box A285, Sydney South, NSW 2000 Australia
** Marmion Marine Laboratories, CSIRO Division of Fisheries
P.O. Box 20, North Beach WA 6020 Australia

ABSTRACT

A series of quantitative infaunal samples were taken between February 1989 and July 1991 at 10 sites in Jervis Bay, a protected marine embayment on the south coast of New South Wales. Six sites had muddy/sand sediments and four sites were in beds of the seagrass *Posidonia australis*. Replicate samples were taken at each site in every time period to produce a quantitative baseline with estimates of variability. This baseline can be used to assess future changes in the infaunal assemblages in Jervis Bay. Polychaetes were a major component of the fauna in terms of numbers of individuals and numbers of species. The polychaete fauna was represented by 171 species in 36 families. Assemblage data were analysed using multivariate classifications. Assemblages tended to differ between the two habitats and among some sites within a habitat. These differences remained stable through time. Some species were widely distributed across sites and habitats, and the patterns in assemblage composition were due primarily to the restricted distribution of some rarer species. Density data for the dominant polychaete species were used in analysis of variance in an attempt to assess spatial and temporal patterns in their abundances. Densities of most species varied in a complex manner with spatial patterns being more obvious than temporal ones. Patterns in abundance are difficult to explain or predict because of the limited information available on life histories of these or related species and the absence of similar studies conducted elsewhere.

RÉSUMÉ

**Structures temporelles et spatiales de la distribution des Polychètes endogées de la baie de Jervis, Nouvelles Galles du Sud, Australie**

Une étude quantitative de l'endofaune de substrat meuble a été réalisée sur la côte Sud du NSW (Australie) à Jervis Bay, une baie peu profonde et protégée de la houle. Dix stations ont été échantillonnées ; quatre au sein de l'herbier de *Posidonia australis* et six en dehors de l'herbier. Les prélèvements ont été effectués tous les quatre mois de février 1989 à juillet 1991. Les Polychètes sont, en nombre d'espèces et en nombre d'individus, les organismes les plus abondants de cette endofaune : 36 familles et 171 espèces ont été identifiées. Toutes les données ont été traitées avec le "Pattern Analysis Package". Il en ressort que les replicats d'un même substrat tendent à fusionner, indiquant ainsi la prépondérance du facteur site sur le facteur saison. Une analyse de variance portant sur les principales espèces de Polychètes montre que si les facteurs sites ou saisons sont prépondérants pour la distribution de nombreuses espèces, ils agissent aussi en synergie. Ces modèles de distribution sont

HUTCHINGS, P.A. & C.A. JACOBY, 1994. — Temporal and spatial patterns in the distribution of infaunal Polychaetes in Jervis Bay, New South Wales, Australia. *In:* J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 441-452. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

discutés en détail en tenant compte des faibles données existant sur le cycle de vie de ces espèces. Les résultats obtenus sont également comparés à ceux fournis par des études similaires réalisées dans d'autre régions du monde, rien de comparable n'ayant été fait en Australie.

## INTRODUCTION

Jervis Bay, a temperate marine embayment on the south coast of New South Wales, is highly regarded for its environmental quality and is listed on the Register of the National Estate. The bay is currently used for tourism, commercial and recreational fishing and Department of Defence training exercises. Population growth in the surrounding area is increasing. Concern about the possible impacts of current uses and proposed additional uses led the Department of Defence to fund a three year program of inventory and baseline studies (WARD & JACOBY, 1992). One of these studies aimed to quantify spatial and temporal patterns in the abundances of infauna in the muddy/sand and vegetated sediments around the Bay. This paper discusses the preliminary findings from this study with an emphasis on polychaetes, which were a major component of the infauna and an essential part of any baseline that characterises the existing status of Jervis Bay.

## METHODS

Jervis Bay (35°08'S, 150°45'E) is a kidney-shaped marine embayment. It reaches a maximum depth of about 30 m, has a surface area of 102 km$^2$, and opens onto the continental shelf through a 3.5 km wide entrance. The bay has a relatively small catchment which does not contain a major river but does include several small creeks. Mangroves and saltmarshes line these creeks. The shores of the bay are primarily sandy beaches bounded by creek mouths and shallow rocky reefs. Extensive beds of seagrass *Posidonia australis* occur in the shallow, subtidal areas (above 10 m) in the northern and southern parts of the bay. Beyond the rocky reefs and seagrasses (below 10 m), are characterised by extensive muddy/sand areas.

Four sites were selected in *P. australis* beds (vegetated sites) and six were chosen in deeper, muddy/sand sediments (Fig. 1). Depths at the vegetated sites varied in depth from 2–6 m (Callala Boat Ramp 2 m, Hare Bay 3 m, Green Island 6 m and Hole in the Wall 5 m). Four muddy/sand sites, Hole in the Wall, Montague Roadsted, Green Point and Plantation Point 'shallow', were at 12 m and two sites, Honeymoon Bay and Plantation Point 'deep' were at 20 m.

Nine sets of infaunal samples were collected at each site between February 1989 and June 1991. Sampling periods were separated by two to five months. At each vegetated site, infauna were collected by SCUBA divers using a hand operated corer (11 cm internal diameter; surface area of 0.01 m$^2$). Four replicates were collected from each of two plots (2 m x 2 m) separated by about 50 m. At muddy/sand sites, five replicate samples were collected using a Smith-McIntyre grab (sampling area 0.06 m$^2$). All samples were put into bags made of 1.0 mm mesh, washed, stained with Biebricht Scarlet and fixed in 7 % neutralised formalin. In the laboratory, animals were extracted, identified and counted. The mesh size was selected after consideration of time and funds available for sorting and the main objective of the study, i.e., description of the overal distribution and abundance of the benthic macroinfauna within the bay.

Assemblage data were analysed to assess spatial and temporal patterns in species composition. All data were $\log_{10}(x + 1)$ transformed prior to analyses. Multivariate classifications were based on Bray–Curtis dissimilarity measures (BELBIN, 1989). These measures were classified by hierarchical, polythetic, agglomerative fusion using unweighted pair group arithmetic averaging (UPGMA), with no order or adjacency constraints and a beta coefficient of - 0.01). The results of the fusion were used to construct a dendrogram from which groups of samples were defined on the basis of fusion patterns. In addition, multivariate classifications of species according to their occurrences in samples were conducted using two–step dissimilarity measures in a UPGMA fusion with no constraints on adjacency or order and a beta of – 0.01 (BELBIN, 1989). Species groups were defined from a dendrogram constructed from the results of the classification. The relationships between species groups and site groups were examined using two–way tables.

Spatial and temporal patterns in the distribution of common species were investigated using univariate analyses of variance. The ANOVAs based on data from grab samples had sampling periods and sites as random factors. The ANOVAs based on core samples, also had sampling periods and sites as random factors, as well as, plots as a random factor nested within sites. Prior to conducting the ANOVAs, data were tested for homogeneity

Source : MNHN, Paris

of variance using Cochran's test. All data required $\log_{10}(x+1)$ transformation to achieve homoscedasticity. Some data remained heterogeneous, and these data were not analysed.

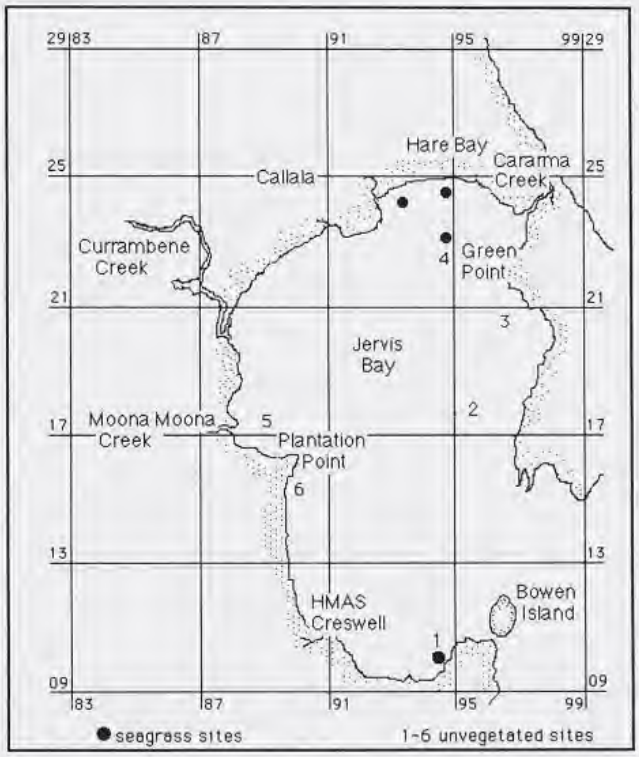



FIG. 1. — Map of Jervis Bay showing location of vegetated and muddy/sand sites. Site 1, Hole in the Wall; Site 2, Honeymoon Bay, Site 3; Montague Roadsted; Site 4, Green Point and Site 5, Plantation Point "shallow"; Site 6, Plantation Point "deep".

## RESULTS

Over 630 infaunal species were collected, including 248 crustaceans, 197 molluscs, 171 polychaetes and 15 echinoderms as well as representatives of Nemertea, Sipuncula, Phoronida, Turbellaria and Coelenterata which were not identified to species. A majority of the 171 species of polychaetes (representing 31 families) have previously been recorded from New South Wales waters (HUTCHINGS & MURRAY, 1984).

Analyses were confined to a data set composed of counts of polychaetes, molluscs, and echinoderms from nine sampling periods. To date, crustaceans have been identified only in the first four sets of samples.

A series of classifications were performed. Initially, a multivariate analysis, was performed using 558 replicates as separate samples. The resulting distribution of dissimilarity measures was strongly skewed towards high values which suggests that single replicate samples varied greatly. It is unlikely that single samples adequately represented an assemblage; therefore replicate samples from each combination of site and time periods were summed (i.e., n = 5 for grab samples and n = 8 for core samples) and the analysis was repeated. This classification revealed a strong dissimilarity between core and grab samples, i.e., samples from vegetated and muddy/sand sites. This dissimilarity may have been partly due to biases introduced by the two different types of sampling gear. These biases will be investigated in a separate paper. Subsequent analyses considered samples from vegetated and muddy/sand sites separately.

Source : MNHN, Paris

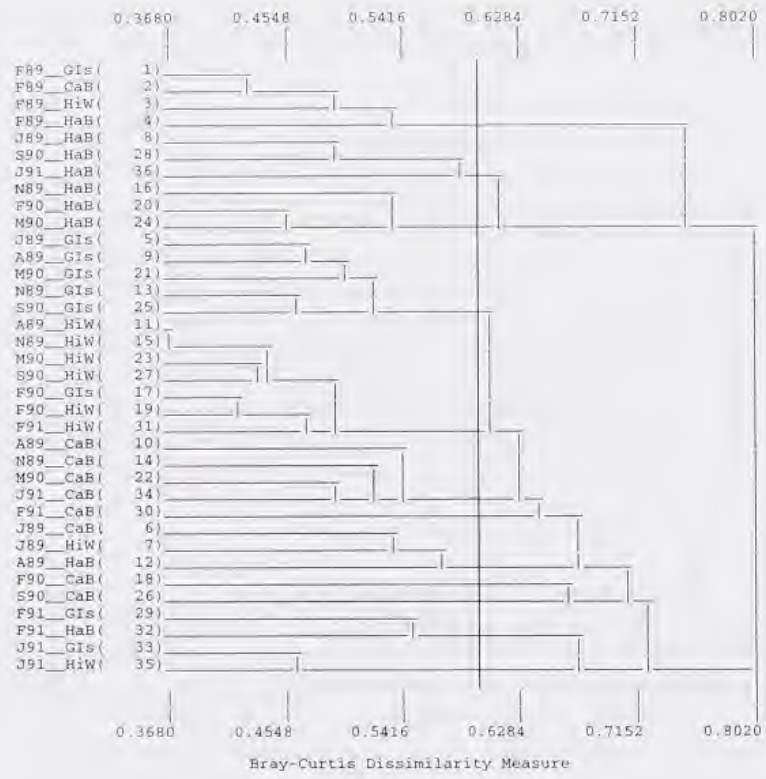



FIG. 2. — The results of the fusion generated by multivariate classifications based on Bray–Curtis dissimilarity measures, for the vegetated core sites. F= February, J= June, A= August, N= November, M= May, S= September, 89 = 1989, 90 = 1990, 91 = 1991, GIs–Green Island, CaB–Callala Boat Ramp, HaB–Hare Bay, HiW–Hole in the Wall.

Separate classifications based on data from grab and cores revealed that species composition differed primarily among sites and was reasonably stable among sampling times (Figs 2 & 3). Exceptions were the February 1989 core samples which had relatively unique species composition regardless of their site of origin (Fig. 2). The grab samples from shallow (12 m) muddy/sand sites (Hole in the Wall, Green Point and Montague Roadsted) tended to group together (Fig. 3). All the samples from Plantation Point deep (20 m) and most of the samples from Honeymoon Bay (20 m), formed distinct groups (Fig. 3). The overall species composition of these two sets of samples were clearly different from those found in the samples taken at the other muddy/sand sites (Fig. 3).

The distribution of species which led to differentiation of site groups were determined by examining two-way tables. These tables showed that many species were abundant at all sites. Site groups were most clearly characterised by a few rare species with restricted distributions.

Assemblage composition did not show change dramatically through time, but the abundances of individual species may have varied between sampling periods. Univariate ANOVAs provided a means of assessing these variations. More than 25 % of the species recorded from the 558 samples were represented by less than 10 individuals, but some polychaete species were present in sufficient samples for detailed analyses of their distribution among sites and through time. Following Cochran's tests, data for three species from core samples and five from grab samples were examined using ANOVAs.

Analyses of variance indicated that the densities varied among combinations of sampling time and site. The exceptions were *Eunice australis* and *Owenia fusiformis* from vegetated sites. Their densities varied significantly only with time. Our knowledge of the reproductive biology of these common species, or their relatives, is limited, and this makes predictions or interpretations of temporal patterns in abundances difficult. Some preliminary comments can be made.

Source : MNHN, Paris

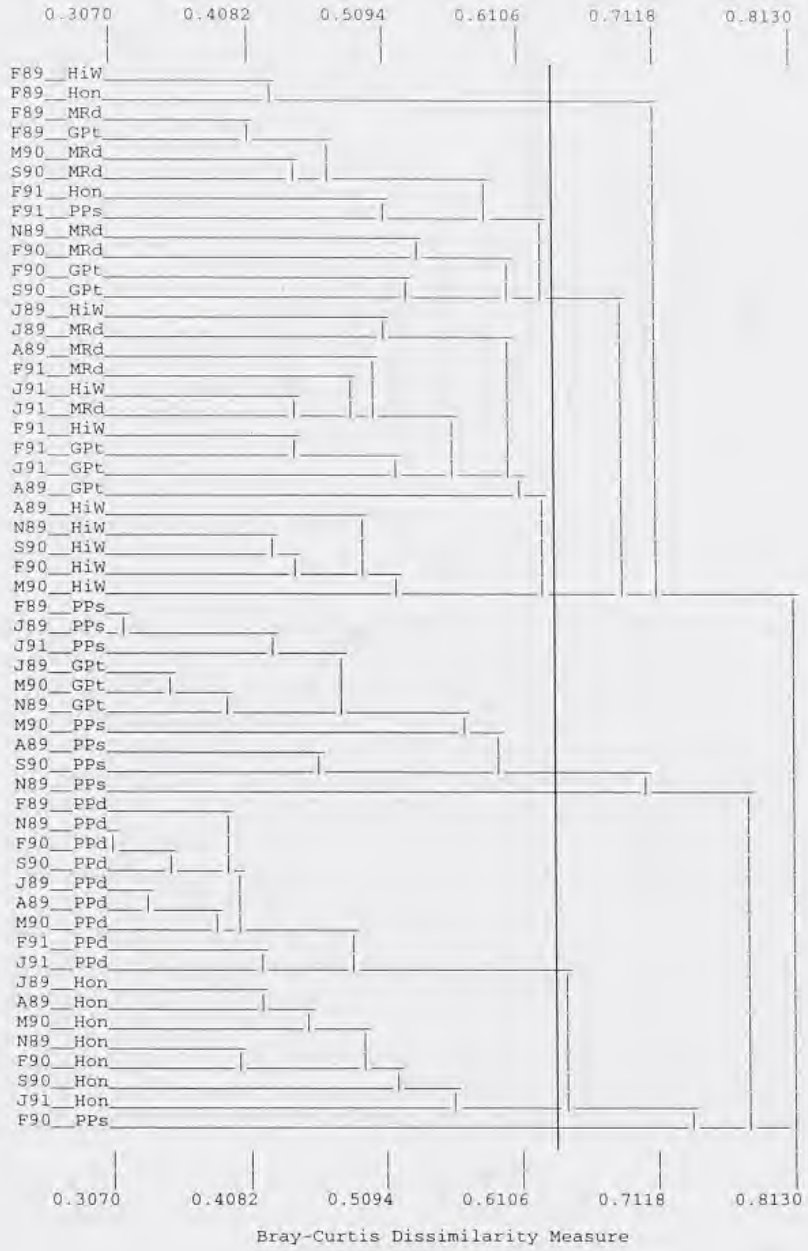



FIG. 3. — The results of the fusion generated by multivariate classifications based on Bray–Curtis dissimilarity measures, for the muddy/sand grab sites. F= February, J= June, A= August, N= November, M= May, S= September, 89 = 1989, 90 = 1990, 91 = 1991, HiW–Hole in the Wall, Hon–Honeymoon Bay, MRd–Montague Roadsted, GPt–Green Point, PPs–Plantation Point "shallow", PPd–Plantation Point "deep".

*Eunice australis* was taken primarily in core samples. All four sites had relatively high numbers in the summer (February) and spring (November) of 1989, but the overal mean density of *Eunice* was always low (Fig. 4). This makes interpretations of temporal patterns difficult. *Eunice australis* probably breeds annually after reaching

Source : MNHN, Paris

maturity in its second year. It is almost certainly a broadcaster and recruits by pelagic larvae. The life–span of this species is greater than one year, which may explain why some individuals were always present in the vegetated core samples although numbers varied over time. If increases in numbers were due to recruitment, it appeared to be poor in 1991.

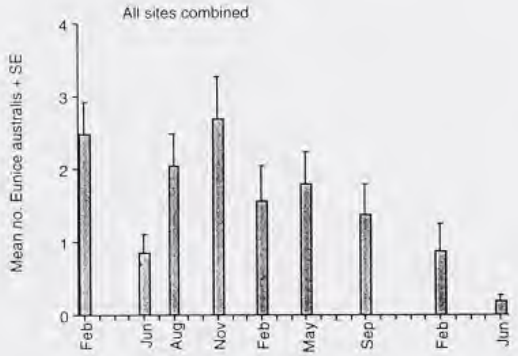



FIG. 4. — The mean numbers of *Eunice australis* present at all vegetated sites on nine occasions between February 1989 and June 1991.

*Owenia fusiformis* was recorded from both vegetated and muddy/sand sites. Peaks numbers of individuals were observed at all four vegetated sites in February of 1989, 1990 and 1991. The mean densities of *Owenia* were low, which complicates interpretations of variations in mean density. Densities of this species were higher in samples from muddy/sand sites, with the highest densities recorded in samples from the deeper sites. Numbers of *Owenia* taken from the muddy/sand sites fluctuated over time, but no consistent pattern were evident. Temporal patterns in abundance are difficult to predict because nothing is known about the reproduction of this species. It probably breeds annually by broadcasting because evidence of brooding was never observed when individuals were extracted from their tubes, and it probably recruits via pelagic larvae. *Owenia fusiformis* is currently regarded as a cosmopolitan species, but a detailed study of the genus *Owenia* in Australia may disprove this and reveal one or more undescribed species. All specimens collected in Jervis Bay appeared to belong to one species.

*Notomastus chrysosetus* was taken in greatest numbers from vegetated sediments at Hole in the Wall (Fig. 5). At this site, numbers tended to be slightly higher in the summer (February) and spring (November) of the first year. If these peaks were due to recruitment, the data suggest that there was little recruitment in 1991. This species probably breeds annually and produces a benthonic larval stage with limited ability to disperse.

*Magelona* sp.1 was present primarily in the muddy/sand sediments at the 'deep' and 'shallow' sites at Plantation Point. Its numbers fluctuated through time without a clear pattern. Further research is needed to clarify the biological significance of temporal variations in numbers of this species and to identify the factors that appear to limit its distribution to certain sites.

*Nephtys inornata* was taken primarily at five of the six muddy/sand sites. Densities tended to vary with time in an unpatterned way, although samples from all muddy/sand sites showed an increase in numbers during February 1991 (Fig. 6). This suggests that widespread recruitment may have occurred prior to this time. There was some evidence that recruitment had occurred in the summer during the two previous years, but only at some sites (Fig. 6). *Nephtys* is almost certainly an annual breeder with mass spawning giving rise to pelagic larvae. Our data suggest that levels of successful recruitment varied among years and locations.

*Augeneria verdis* was found primarily in the muddy/sand sediments with numbers varying inconsistently over time (Fig. 7). Honeymoon Bay always had the lowest number of individuals present (Fig. 7). Although studies have not been undertaken on the reproductive strategies employed by this species or related ones, we suspect that it breeds annually by broadcasting and recruits via pelagic larvae.

*Mediomastus* n.sp., was referred to as *Mediomastus californiensis* in earlier reports (CSIRO, 1991) and by HUTCHINGS & MURRAY (1984) but it is a new species of *Mediomastus,* which is being described by WARREN *et al.* (in press). *Mediomastus* n.sp. occurred predominantly at the six muddy/sand sites (Fig. 8). During at least one sampling period, mean densities were above 10 at all sites, except Plantation Point 'shallow'. Densities of this species increased in February or May 1990 at all sites except Plantation Point 'shallow' (Fig. 8). Recruitment may

Source : MNHN, Paris

have occurred at this time. We suspect that this small species (5–10 mm in length) breeds annually, produces few

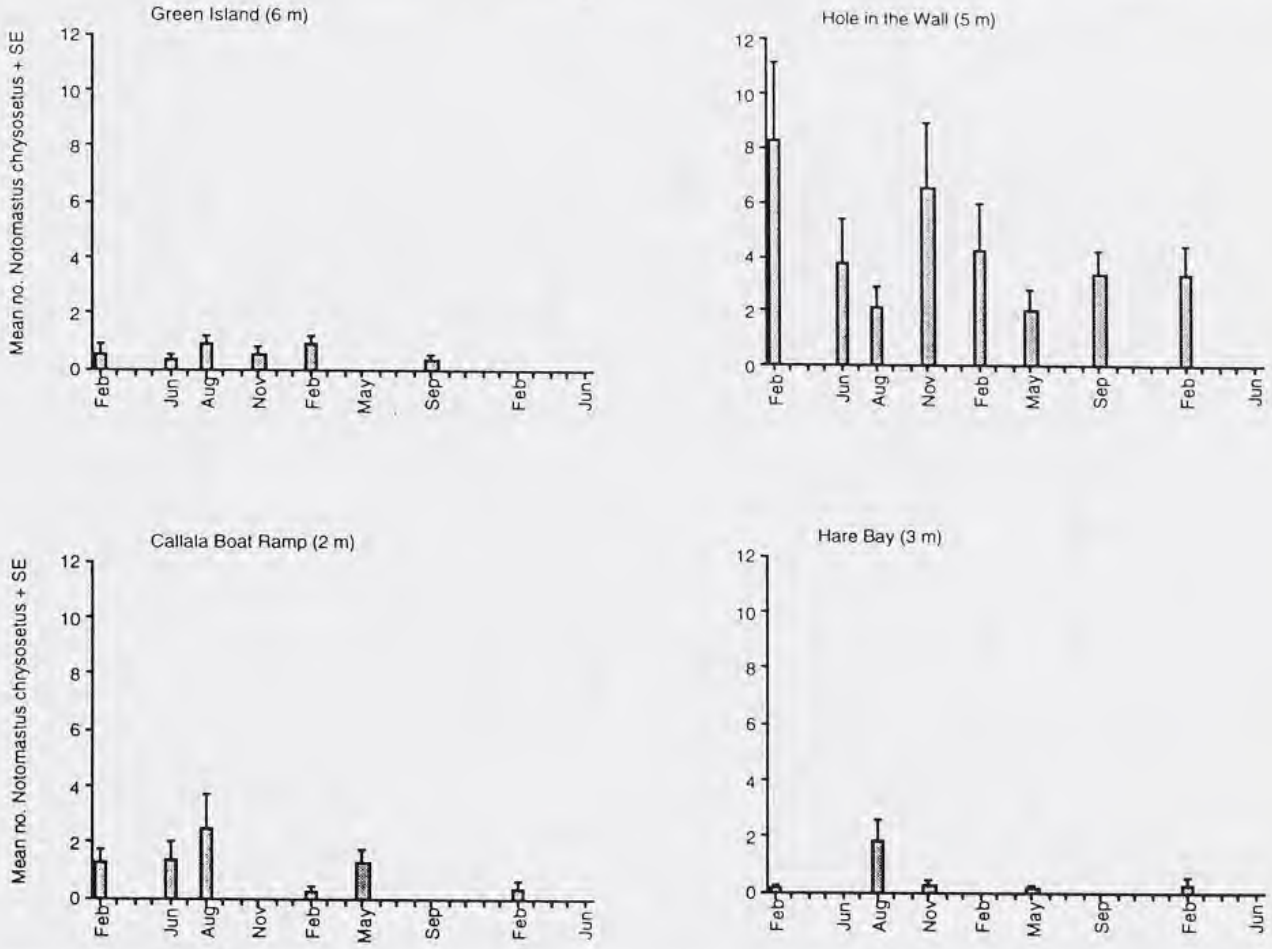



FIG. 5. — The mean numbers of *Notomastus chrysosetosus* present at all the vegetated sites on nine occasions between February 1989 and June 1991.

gametes and does not survive spawning. Judging from the protracted period of increased numbers, the breeding season may be fairly extended. In addition, it may have been several weeks after settlement before new recruits would have been sampled by our techniques, and this may explain why the increase in numbers were spread over several months.

## DISCUSSION

Both types of analyses indicated that the densities of polychaetes and other infauna varied in a more consistent manner among sites than among sampling times. The species composition of the infauna from muddy/sand sediments appeared to vary between the two depths that were sampled. Multivariate analyses indicated that differentiation among sites at different depths was due mainly to the distributions of less abundant species, and *Owenia fusiformis* also followed this trend. Although the results are not reported here, a tendency for species composition to vary among sites and remain similar at a site through time was also seen when data for molluscs and echinoderms were included in the analyses.

It appeared that many species occurred in both vegetated and muddy/sand sites, but muddy/sand sites generally yielded more species. This trend may be partly due to the different sampling techniques employed in the different habitats.

Source : MNHN, Paris

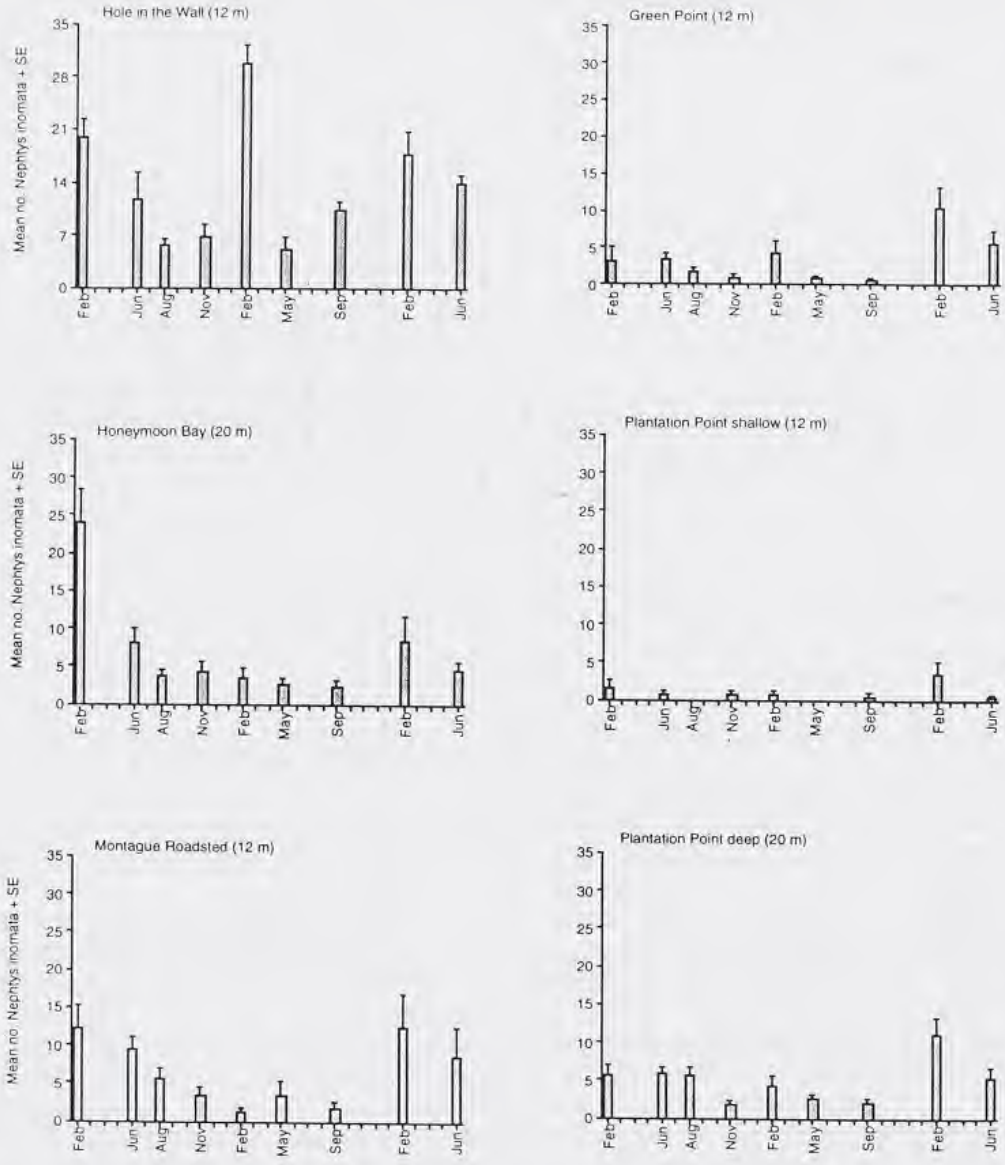



FIG. 6. — The mean numbers of *Nephtys inornata* present at each of the muddy/sand sites on nine occasions between February 1989 and June 1991.

The majority of polychaete species were not sufficiently numerous or common for analyses of their distributions over time. Of the 171 species, only seven were common enough for univariate analyses. Temporal variation in densities of common species would be due to a combination of recruitment and mortality of older individuals. The available data do not provide strong evidence for consistent patterns in these events either within or among years. Evidence of temporal patterns in mortality could be obtained by examining the size classes represented in the samples. All material has been retained for future examinations. Direct evidence of recruitment was not expected because recruits of most species are too small to have been retained by the 1.0 mm mesh employed during this study. The mesh size used was the most appropriate for determining the overall distribution and abundance of infauna, the primary goal of this study. Two hypotheses suggested by the results of this study are: (1) polychaete recruitment is not equal at sites separated by a few kilometres and (2) many species of polychaetes recruit annually but the intensity varies among years.

Source : MNHN, Paris

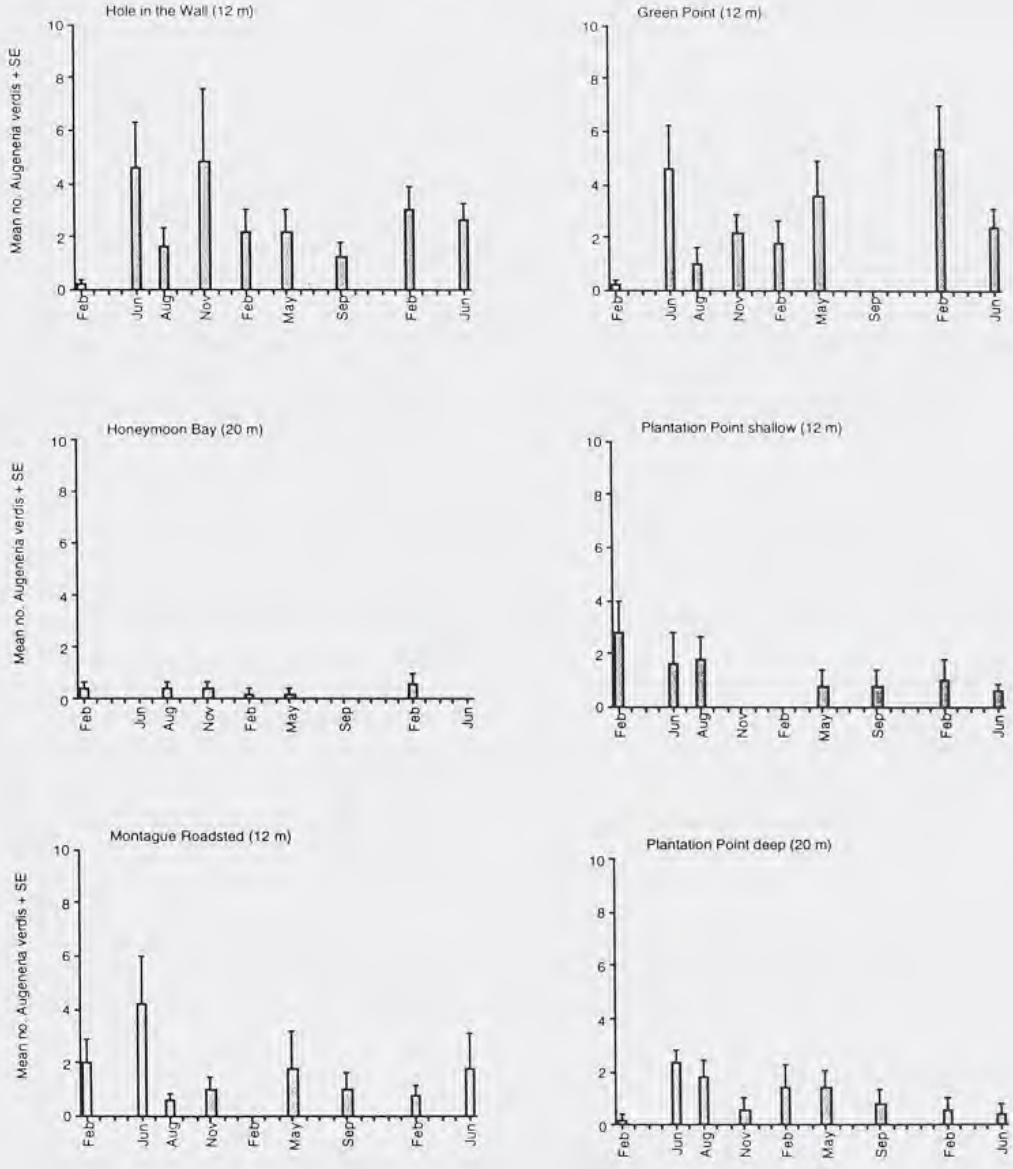



FIG. 7. — The mean numbers of *Augeneria verdis* present at all muddy/sand sites on nine occasions between February 1989 and June 1991.

Multivariate analyses also indicated that the polychaete fauna differed between vegetated and muddy/sand sites. Samples from vegetated sites contained a subset of the suite of species which occurred in the muddy/sand sites.

The study also highlights the need for more information on the reproductive strategies of these common species in Jervis Bay. In all cases we have put forward our opinion of their reproductive strategies on the basis of what is known for related species and, in some cases, information on egg sizes observed for these species either in individuals from Jervis Bay or elsewhere in southern Australia.

Source : MNHN, Paris

All the common species in Jervis Bay have been found in vegetated and muddy/sand sediments throughout southern Australia (HUTCHINGS & MURRAY, 1984). Although the number of quantitative studies conducted in southern Australia has increased considerably over the past 20 years no other studies have examined changes in the densities of individual species over time.

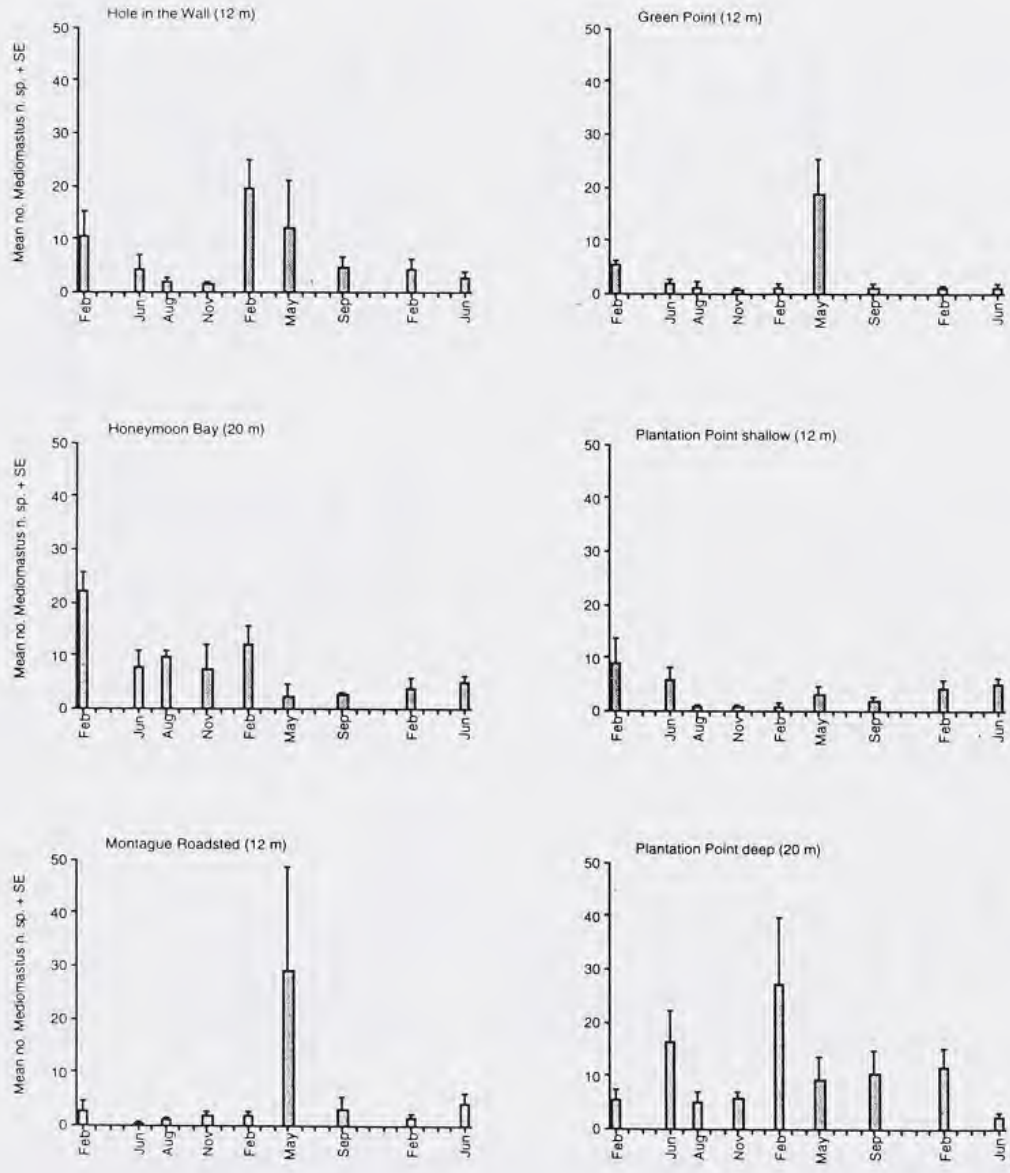



FIG. 8. — The mean numbers of *Mediomastus n.sp.* present at all the muddy/sand sites on nine occasions between February 1989 and June 1991.

STEPHENSON *et al.* (1974, 1977) sampled the benthos of Moreton Bay, in southern Queensland on a regular basis over many years and they found that changes in the composition of the fauna between years was more important than seasonal changes, and that sporadic floods were a major force structuring these communities. In a

Source : MNHN, Paris

subsequent study STEPHENSON (1980) found that the benthic community changed over time with the frequency of change varying between sites. A 3 year cycle was typical at inshore sites and 5.5 year cycles were found at the more oceanic sites. Changes in density of individual species were not examined in detail. After more than a decade of intensive sampling, STEPHENSON *et al.* (1977) were unable to predict community structure and they stressed the unpredictability of the species composition of these benthic communities. Our studies in Jervis Bay would generally support these conclusions, although we suggest that all sites (both vegetated and muddy/sand) had a core of common species. Variation in the communities was due to a number of rarer species. The exact composition of an assemblage may be largely determined by chance recruitment events of the rare species. These recruitment events are presumably influenced by factors such as local water flow patterns and sediment characteristics, as well as the supply of larvae and the interactions with the existing suite of species at a particular site. The widely distributed species in Jervis Bay were relatively long–lived. Recruitment failure in one of the three years that made up this study may not have appeared as a change in adult populations.

No other studies of the temporal or spatial variations in the infaunal communities have been undertaken in Australian seagrass beds (HOWARD *et al.*, 1989). This is despite their importance as nursery habitats for commercial species of fish and prawns (BELL & POLLARD, 1989). GAMBI *et al.* (1991) published an abstract describing a study of spatial and temporal patterns in polychaete distributions in Mediterranean beds of *Posidonia oceanica*, but the complete paper has yet to be published so a comparison with our findings can not be made. Similar studies have not been undertaken elsewhere in the world, in part because of taxonomic difficulties. A recent study by CROUCH (1991) investigated the polychaetes associated with the rocky intertidal surfgrass *Phyllosadix scouleri* and *P. torreyi* in California, however this represents a very different environment to *Posidonia australis* communities, and therefore her findings have little relevance to this study. Hopefully this lack of knowledge of *Posidonia* communities will change in the future. The Australian Museum is currently sampling the muddy/sand sediments of Botany Bay (another sheltered bay about 100 km north of Jervis Bay) over an extended period of time. This study is revealing a fauna similar to that found in Jervis Bay and detailed comparisons will be made once this study is completed.

This study has provided a detailed baseline for the distribution and abundance of macroinfauna in Jervis Bay. The baseline will facilitate management of the bay including a recently declared Australian Marine National Park and a proposed New South Wales Aquatic Reserve. A program of long–term monitoring may be introduced in Jervis Bay, and this study could act as a basis for the design of a benthic monitoring program.

## ACKNOWLEDGMENTS

We should like to thank the Department of Defence for funding this project through CSIRO Division of Fisheries. Angela MEZA, Fiona MCKILLUP and Rob PATTERSON, assisted in the collection and sorting of this material. Cassie ROSE and Angela MEZA assisted in the analyses of the data.

## REFERENCES

BELL, J.D & POLLARD, D.A., 1989. — Ecology of fish assemblages and fisheries associated with seagrasses. *In*: A.W.D. LARKUM, A.J. MCCOMB & S.A. SHEPHERD (eds), *Seagrasses: Treatise on the Biology of Seagrasses with special reference to the Australasian Region*. Elsevier, Amsterdam : 565-609.

BELBIN, L., 1989. — *PATN Pattern Analysis Package. Technical Reference*. CSIRO Division of Wildlife and Ecology, 222 pp.

CROUCH, C.A., 1991. — Infaunal polychaetes of a rocky intertidal surfgrass bed in southern California. *Bull. mar. Sci.*, **48** :386–394.

CSIRO.,1991. — *Jervis Bay Baseline Studies, Progress Report, December 1991*. CSIRO Division of Fisheries, Jervis Bay.

GAMBI, M.C., GIANGRANDE, A., MARTINELLI, M & CHESSA, L.A., 1991. — Polychaetes of the Mediterranean seagrass *Posidonia oceanica*: Spatio–temporal distribution and feeding guilds analysis. *Bull. mar. Sci.*, **48**(2) : 596 p.

HOWARD, R.K., EDGAR, G.H. & HUTCHINGS, P.A.,1989. — Faunal assemblages of seagrass beds. *In*: A.W.D. LARKUM, A.J. MCCOMB & S.A. SHEPHERD (eds), *Seagrasses: Treatise on the Biology of Seagrasses with special reference to the Australasian Region*. Elsevier, Amsterdam : 536-582.

HUTCHINGS, P.A. & MURRAY, A., 1984. — Taxonomy of polychaetes from the Hawkesbury River and the southern estuaries of New South Wales. *Rec. Aust. Mus.*, **36** (suppl.3) : 1–119.

STEPHENSON, W., 1980. — Time patterns of macrobenthic species in Moreton Bay. *Aust. J. Ecol.*, **5** : 245–262.

Source : MNHN, Paris

STEPHENSON, W., COOK, S.D & RAPHAEL, Y.I., 1977. — The effects of a major flood on the macrobenthos of Bramble Bay, Queensland. *Mem. Qd. Mus.*, **18** :9 8–119.

STEPHENSON, W., WILLIAMS, W.T. & COOK, S.D., 1974. — The benthic fauna of soft bottoms, southern Moreton Bay. *Mem. Qd. Mus.*, **17** :73–123.

WARD, T.J. & JACOBY, C.A., 1992. — A strategy for assessment and management of marine ecosystems: baseline and monitoring studies in Jervis Bay, a temperate Australian embayment. *Mar. Poll. Bull.*, **25** : 163–171.

WARREN, L.M., HUTCHINGS, P.A & DOYLE, S. (in press). — A revision of the genus *Mediomastus* Hartman, 1947 (Polychaeta: Capitellidae). *Rec. Aust. Mus.*

Source : MNHN, Paris

# Ecology and biogeochemistry of *Paralvinella sulfincola* at northeast Pacific hydrothermal vents: review and comparison with *Alvinella* spp. of the east Pacific rise

*S. Kim JUNIPER*

Géotop & Département des Sciences Biologiques
Université du Québec à Montréal
C.P. 8888, succ. A, Montréal (Québec)
H3C 3P8 Canada

ABSTRACT

The "sulfide worm" *Paralvinella sulfincola* Desbruyères & Laubier 1993, of northeast Pacific hydrothermal vents, builds a mucous tube on the surface of high temperature chimneys, as does *Alvinella* spp. on the East Pacific Rise. *P. sulfincola* is a deposit feeder and likely grazes on thermophilic chimney bacteria. It is argued that deposit feeding is also the primary source of nutrition for *Alvinella* spp. The influence of both worms on the sulfur cycle and on chimney mineralization processes is discussed. While *Alvinella* appears to be more elaborate in its adaptations to the high temperature chimney environment, the functional significance of some of these apparent adaptations remains unclear. Observed effects of *P. sulfincola* on chimney mineralization suggest that the question of how *Alvinella* spp. influences chimney growth patterns needs to be re-addressed. Two previously proposed roles for the epibiotic bacteria in *Alvinella* spp., nutrition and detoxification, can be accomplished by *P. sulfincola* without the aid of episymbionts. This is a strong argument for a re-evaluation of the nature of the *Alvinella*-bacteria symbiosis.

RÉSUMÉ

**Ecologie et biogéochimie du ver *Paralvinella sulfincola* des sources hydrothermales du Pacifique Nord-Est : revue et comparaison avec le genre *Alvinella* de la dorsale du Pacifique oriental**

De façon identique aux *Alvinella* spp. présents au niveau de la dorsale du Pacifique oriental, le «ver sulfure», *Paralvinella sulfincola*, des sources hydrothermales situées dans le Pacifique Nord-Est, construit un tube de mucus à la limite des évents des cheminées d'où jaillit le fluide hydrothermal à haute température. Détritivore, *P. sulfincola* broute probablement des bactéries thermophiles présentes sur les cheminées. Pour *Alvinella* spp., l'alimentation détritique pourrait aussi être la source principale de nourriture. L'influence des deux vers sur le cycle du soufre et sur la minéralisation des cheminées est analysée. Bien que les *Alvinella* spp. semblent être mieux adaptés à un environnement de températures extrêmes, la fonction de certaines de ses adaptations apparentes n'est pas encore claire. Les effets observés de *P. sulfincola* sur la minéralisation des cheminées suggè-

JUNIPER, S.K., 1994. — Ecology and Biogeochemistry of *Paralvinella sulfincola* at Northeast Pacific Hydrotermal Vents: Review and Comparison with *Alvinella* spp. of the East Pacific Rise. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 453-462. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

rent que toute la question de l'influence d'*Alvinella* spp. sur la croissance des cheminées a besoin d'être reformulée. Ainsi, les deux rôles envisagés pour les bactéries épibiotiques chez *Alvinella* spp., soit la nutrition et la détoxification, peuvent être accomplis par *P. sulfincola* sans l'aide d'épisymbiontes. Ceci est un argument important qui entraîne le réexamen de la nature de la symbiose d'*Alvinella* avec les bactéries.

## INTRODUCTION

Since the discovery of hydrothermal vent biological communities in 1977, numerous new vent-specific species have been described, many of which have unusual adaptations for bacterial-invertebrate symbiosis and for life at high temperatures. The intimate association of several species with mineral deposition processes has inspired studies of biomineralization (JUNIPER *et al.*, 1988, 1992). High temperature microorganisms have been the focus for most work on sulfide chimneys. In addition to thermophilic and ultra-thermophilic bacteria that grow within the plumbing system of chimneys and on chimney surfaces, a specialized chimney fauna flourishes in this extreme and rapidly changing environment (TUNNICLIFFE & JUNIPER, 1990). Adaptations of the chimney fauna to its habitat and its influence on mineralization processes are newly emerging areas of research.

Among the first organisms to colonize newly-formed chimney surfaces are the alvinellid worms (JUNIPER *et al.*, 1992). At northeast Pacific vent sites, the "sulfide worm", *Paralvinella sulfincola* Desbruyères and Laubier (1993) [*in* TUNNICLIFFE *et al.*, 1993], occupies a niche similar to that of *Alvinella pompejana* and *A. caudata* and occasionally *Paralvinella grasslei* on the East Pacific Rise (EPR) (DESBRUYÈRES *et al.*, 1985; DESBRUYÈRES & LAUBIER, 1986; TUNNICLIFFE *et al.*, 1993). The sulfide worm was originally thought to be a form of *Paralvinella palmiformis* that colonized environments where mineral precipitation is heavy, forming loose tube structures with its otherwise amorphous mucous secretions (JUNIPER *et al.*, 1988; TUNNICLIFFE & JUNIPER, 1990). Later morphological, genetic and behavioral studies recognized a separate species, *Paralvinella sulfincola* (TUNNICLIFFE *et al.*, 1993). These tube-building worms colonize large areas of newly-formed portions of high-temperature chimneys (JUNIPER *et al.*, 1988; TUNNICLIFFE & JUNIPER, 1990). Ongoing studies reveal a number of physiological, molecular and behavioral adaptions that allow this organism both to tolerate an extreme environment and to exploit the resources present. Other work indicates that the worm can influence mineralization processes on chimney surfaces. This paper develops an overview of the ecology and biogeochemistry of *P. sulfincola* and compares them with the *Alvinella* species to highlight present understanding and future research directions. Since most previous studies on species of *Alvinella* do not distinguish between *A. pompejana* and *A. caudata*, discussion here will generally refer to them as *Alvinella* spp.

## THE HIGH TEMPERATURE CHIMNEY ENVIRONMENT

The smoking chimneys and spires that develop around high temperature vents are the focal points of sulfide mineral precipitation on sediment-starved spreading ridges (HÉKINIAN *et al.*, 1983; HÉKINIAN & FOUQUET, 1985; TIVEY & DELANEY, 1986; HANNINGTON & SCOTT, 1988). Growth of these sulfide edifices passes through two major phases that correspond to changes in the environment of mineral deposition within the chimney structure. HAYMON & KASTNER (1981) and HAYMON (1983) proposed that chimney growth begins when seawater entrained into a jet of high temperature (350 °C) fluid is heated to supersaturation with respect to $CaSO_4$. This causes the precipitation of anhydrite and the upward growth of primitive chimney walls in the form of a porous anhydrite shell. Induration of this shell by further precipitation of anhydrite and other minerals eventually begins to isolate hydrothermal fluid within the structure from surrounding seawater to the point where significant physico-chemical gradients develop across the chimney walls. This initiates the second phase of chimney development. While anhydrite continues to accrete on the outer walls and on the distal portion of the growing chimney, hydrothermal fluids migrate outward through the walls, dissolving and replacing anhydrite with sulfide minerals. At the same time, high-temperature, low-pH conditions within the chimney conduit favor the inward growth of Cu-Fe rich sulfides. Chimneys grow in this manner up to several metres in height, accreting new anhydrite material around the vent orifice, and later infilling and replacing it with sulfides. Not all chimneys form in this way. Instead of anhydrite, direct precipitation of barite or sphalerite can form the early shell (PARADIS *et al.*, 1988). The subsequent processes are essentially the same in all cases. Early walls are replaced and sealed by outflowing hydrothermal fluid that is precipitating sulfide.

The zone of early sulfide mineralization on growing chimneys is the preferred habitat of the sulfide worm (JUNIPER *et al.*, 1988; TUNNICLIFFE & JUNIPER, 1990) (Fig. 1). Prior to worm colonization, a thickening of the

Source : MNHN, Paris

anhydrite walls of the chimney appears be necessary to reduce surface temperatures to levels the worms can tolerate (JUNIPER *et al.*, 1992). TIVEY *et al.* (1990) recorded formation and thickening of an anhydrite shell within a thermistor collar fitted around a smoker orifice. An outer wall temperature of 67 °C was recorded at the end of their experiment. No worms had colonized the shell at that point (M. TIVEY, pers. comm.). It is difficult to define

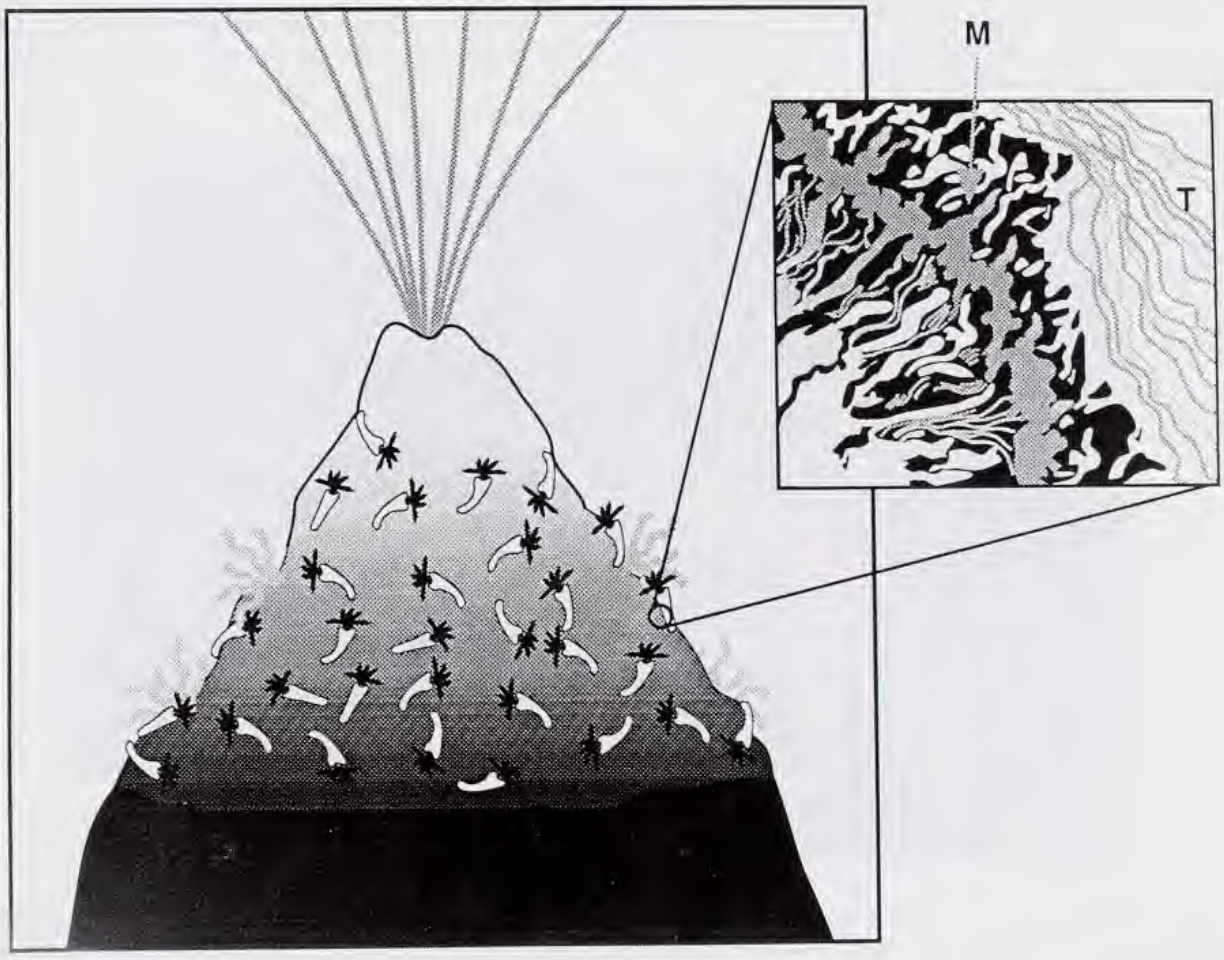



FIG. 1. — Schematic representation of the colonization of high-temperature chimneys by the sulfide worm *Paralvinella sulfincola*. Worms cover extensive surfaces in newly-formed areas of chimney that are undergoing infilling and replacement by sulfide minerals (light shading). Dark shading in lower part of structure represents zone of massive sulfide. Light cap at top indicates a higher temperature zone that is not inhabited by the worms. Insert represents cross-section through chimney wall with location of marcasite crusts (M) indicated beneath worm tubes (T). Right to left in insert is equivalent to moving from the chimney surface toward the interior.

precisely the range of conditions that constitute the worm's habitat. All physico-chemical habitat information must be collected remotely from submersibles, and in this milieu of sharp physico-chemical gradients, remote manipulation of sensors or sampling devices is simply not accurate enough to reliably record conditions within the worm's immediate microenvironment. Temperatures of 20 - 80 °C have been measured on surfaces colonized by sulfide worms (JUNIPER *et al.*, 1992), and it is most likely that the worms regularly experience temperatures within the lower part of this range. *Alvinella* spp. is frequently found at temperatures near 40 °C (FUSTEC *et al.*, 1987) and has recently been reported moving over a 105 °C surface (CHEVALDONNÉ *et al.*, 1992). TUNNICLIFFE *et al.* (1993) emphasize the importance of turbulence and likelihood of occasional blasts of hot water in the upper part of the 20 - 80 °C range.

Source : MNHN, Paris

## TUBE BUILDING

*Paralvinella sulfincola* is one of two northeast Pacific species of *Paralvinella* known to build a tube (Fig. 2). The other species, *P. pandorae*, secretes a thin translucent mucous sheath attached to surfaces such as vestimentiferan tubes (TUNNICLIFFE *et al.*, 1986) The tube of *P. sulfincola* is a more complex multilayered structure (Fig. 3A) that resembles the tube of *Alvinella* spp., although it is less ordered at the ultrastructural level (Fig. 4A) than the tubes of *A. pompejana*. The outer surface of the tube remains soft and not tanned as in *Alvinella* spp., and as a result the tubes tend to aggregate mineral particles. Tube mineral content tends to resemble that of underlying chimney material (JUNIPER *et al.*, 1986).

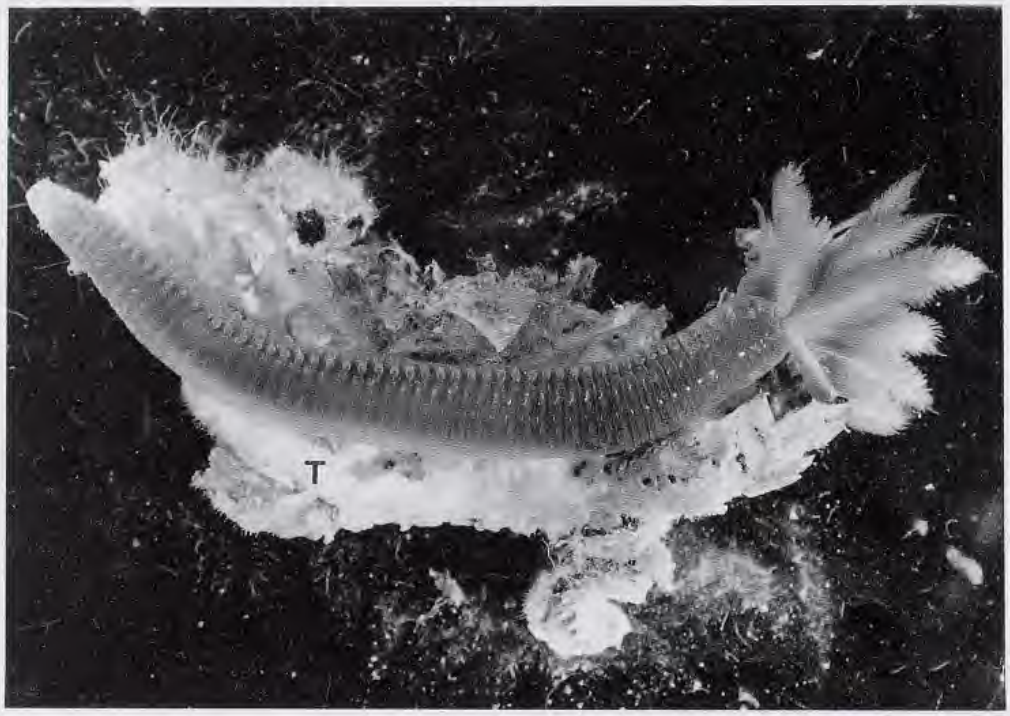



FIG. 2. — Sulfide worm *Paralvinella sulfincola* and its tube (T). In left of photo, bacterial filaments can be seen protruding from edge of tube.

*Alvinella* spp. has an unusual and abundant epibiotic bacterial flora whose biological relationship with the worms is not fully understood (GAILL & HUNT, 1986, DESBRUYÈRES *et al.*, 1983). Large numbers of filamentous bacteria also occur attached to the inner surface of the tubes of *Alvinella* spp. and enclosed within the organic matrix of the tube wall (GAILL *et al.*, 1988; GAILL & HUNT, 1986; GAILL & HUNT, 1991). *P. sulfincola* has a similar abundance of filamentous bacteria within the tube matrix (Fig. 2), but no equivalent epidermal flora. Scanning electron micrographs reveal that both the inner and outer surfaces of the tubes are colonised by filamentous bacteria, with filaments being most abundant on the inner tube surface (Fig. 3B-C). Transmission electron microscopy shows layers of bacteria between consecutive layers of mucus (Fig. 4B). Assuming that new tube layers are added from the inside, the layers of bacteria likely represent cells that were trapped under successive layers of mucus. Bacterial growth on the inner tube wall must alternate with periods of mucus secretion and tube building, as has been suggested for *A. pompejana* (GAILL & HUNT, 1991).

As chimneys grow upward, surfaces colonized by alvinellid worms cool and eventually lose their supply of fluids. Time lapse camera studies have revealed that adult *P. sulfincola* respond to this change in habitat conditions by abandoning their tubes and migrating upward to colonize newly-formed chimney surfaces (JUNIPER *et al.*, 1992; TUNNICLIFFE *et al.*, 1993). Similar conclusions (for *Alvinella* spp.) were reached by FUSTEC (1985) after comparing colonization patterns and chimney dimensions over a three year interval at 13° N on the East Pacific Rise.

Source : MNHN, Paris

## FOOD SOURCES

*Paralvinella sulfincola* is apparently a deposit feeder, using its oral tentacles to gather particles that are then transfered to the mouth (TUNNICLIFFE *et al.*, 1993). Microscopic examination of gut contents reveals grains of sulfide, globules of elemental sulfur and remains of bacterial cells. Bacteria growing on the chimney surface are probably the main source of nutrition. BAROSS & DEMING (1985) observed that bacteria (mainly filamentous forms) are able to colonize most external surfaces of high-temperature sulfide chimneys. Thermophilic bacteria isolated from this habitat include one extreme thermophile isolated from homogenized sulfide worms (PLEDGER & BAROSS, 1989, 1991). Thermophilic or extremely thermophilic bacteria may even represent the principal food source for the sulfide worm, since they are likely the dominant bacteria in this environment (PLEDGER & BAROSS, 1989). If so, this would be the first example of a high-temperature trophic link. While the influence of thermophilic bacteria on geochemical processes is often discussed (BAROSS *et al.*, 1982; JANNASCH & MOTTL, 1985), these organisms are rarely, if ever, considered as a possible food source for metazoans. *Alvinella* spp. is

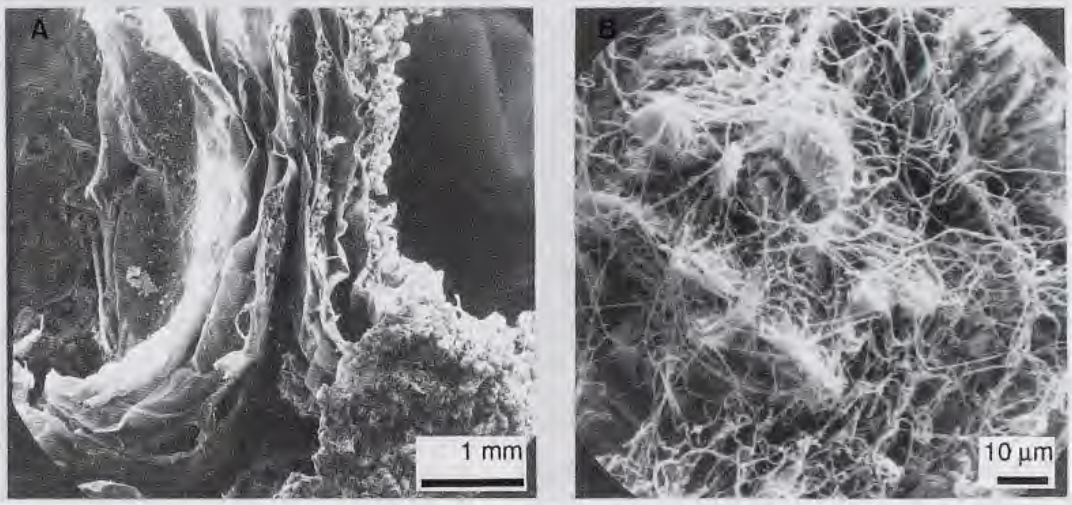



FIG. 3. — Scanning electron micrographs showing layered structure of the tube (end-on view) of *P. sulfincola* (A) and colonization of outer (B) tube surface by bacteria. Outer surface of tube is on right in A.

also known to ingest particles, and this is its most likely mode of nutrition, although the tube bacteria are implicated in a hypothesis concerning a nutrition-related symbiosis with the worm. ALAYSE-DANET *et al.* (1986) proposed that these bacteria secrete dissolved organic matter (DOM) that accumulates within the worm's tube and is subsequently absorbed by *Alvinella* spp. across its epidermal surfaces. They demonstrated incorporation of radioactively labelled compounds by epidermal tissues of *Alvinella* spp. and proposed this as evidence for their hypothesis. However, there are no published data on DOM levels within the tube of *Alvinella* spp. In a study of the digestive tract of *Alvinella pompejana*, SAULNIER-MICHEL *et al.* (1989) note unusual (for polychaetes) evidence for enzymatic breakdown of bacteria in the anterior portion of the digestive tract and suggest that bacterial cells represent an important part of the ingested food. Although they also note an abundance of particulate metals and sulfur in the gut, they do not link this to ingestion of bacteria on chimney particules. Instead, they conclude that the filamentous bacteria inside the alvinellid tubes are the more probable nutritive source (SAULNIER-MICHEL *et al.*, 1989).

## ROLE IN SULFUR TRANSFORMATIONS

The principle effect of *P. sulfincola* on the sulfur cycle at vents may be related to the detoxification of $H_2S$ in the tissues of the worm. Hydrogen sulfide has two main toxic effects: it competes with molecular oxygen for binding sites on haemoglobin molecules, leading to asphyxia, and it destroys the porphyrin structure of cytochrome C in the cellular electron transport system, thereby interfering with energy metabolism (SOMERO *et*

Source : MNHN, Paris

*al.*, 1989). Assays of tissues of *P. sulfincola* have revealed the presence of enzymatic sulfide oxidation (JUNIPER *et al.*, 1992), commonly found in polychaete worms from reducing environments, possibly as a detoxifying agent (SOMERO *et al.*, 1989; VISMANN, 1990). Rates of sulfide oxidation by the worms appear to be high enough to lead to accumulations of elemental sulfur in their mucous secretions and tubes. *Alvinella* spp. accumulates elemental sulfur in its tube and epidermal tissue, presumably also as a result of $H_2S$ detoxification. In this case, the epibiotic bacterial flora has been implicated in sulfide oxidation (LAUBIER *et al.*, 1983), although this activity has yet to be quantified. Sulfide oxidation in the tissues of *Alvinella* spp. also remains unmeasured.

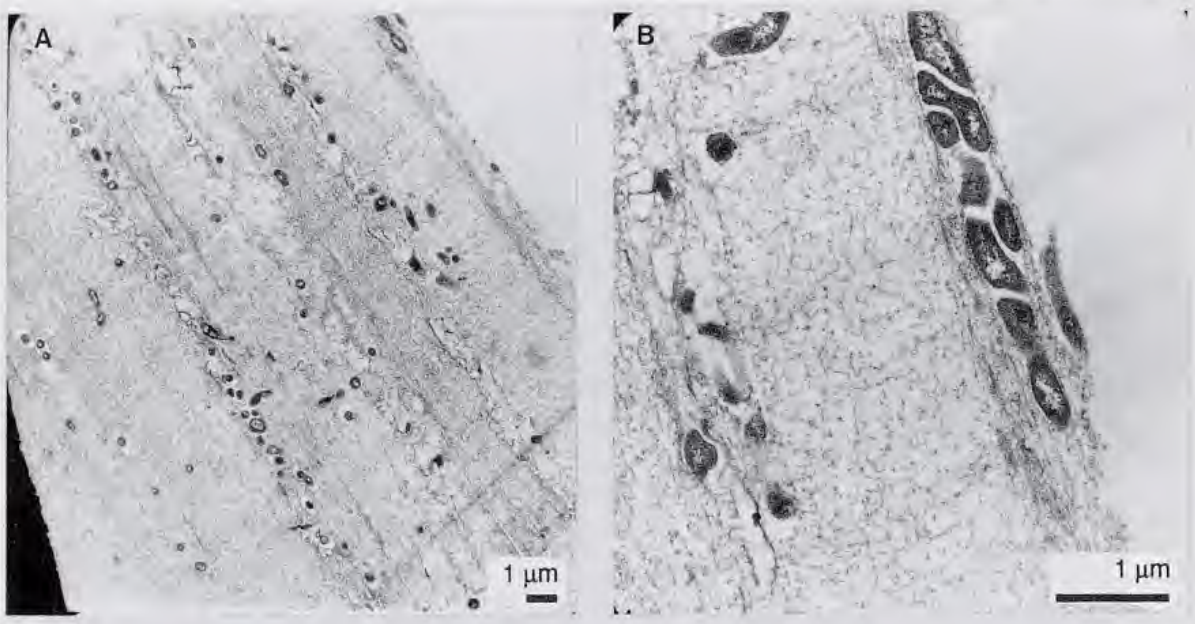



FIG. 4. — Transmission electron micrograph showing layered structure of tube *P. sulfincola* (A) and trapping of bacteria between layers of mucus (B). Tube external surface is on right in both photos.

## EFFECTS ON CHIMNEY MINERALIZATION

Essentially all newly-formed chimney surfaces are colonized by migrating sulfide worms within a matter of days (JUNIPER *et al.*, 1992). The effect of worms on chimney mineralogy was studied by examining the texture and composition of chimney material beneath worm tubes. Sections through the outermost layers of older chimneys generally revealed a 2 mm-thick crust of the sulfide mineral marcasite ($FeS_2$)[1] beneath the mucous tubes (PARADIS *et al.*, 1988; JUNIPER *et al.*, 1992) (Fig. 1). Since the worms generally occur in dense aggregations, the marcasite crust may be extensive enough to affect chimney wall porosity which in turn controls progress of the second stage of chimney mineralization.

The fact that marcasite precipitation is spatially associated with the worm tubes suggests that the worm-bacterial complex alters local geochemistry to favor the precipitation of this mineral. How might this occur ? Formation of both marcasite and pyrite usually requires the presence in solution of intermediate sulfur compounds and FeS precursors; at pH $\leq$ 5 the precipitation of marcasite is favored over that of pyrite (MUROCHICK & BARNES, 1986). High percentage levels of elemental sulfur have been measured in the tube mucus (JUNIPER *et al.*, 1986; JUNIPER, 1988) and similar sulfur concentrations occur in the tubes of *Alvinella pompejana* (GAILL & HUNT, 1986). PARADIS *et al.* (1988) suggested that interaction of $H_2S$ from hydrothermal fluid with this elemental sulfur could form intermediate sulfur compounds such as polysulfide.

[1] Marcasite and pyrite have the same molar ratio of sulfur to iron ($FeS_2$), but their crystallographic characteristics are quite different, as are their physico-chemical properties.

Source : MNHN, Paris

Mineralogical and time-lapse camera data studies provide independent lines of evidence linking tube building to crust formation (JUNIPER *et al.*, 1992; TUNNICLIFFE *et al.*, 1993). As well, the proposed role of tube mucus in this process (PARADIS *et al.*, 1988) is supported by recent experimental work on the formation of iron disulfides from solutions. Reaction of elemental sulfur with water generates high concentrations of thiosulfate, polysulfides and polythionates at the sulfur-water interface (SCHOONEN & BARNES, 1991c). This high local concentration of intermediate sulfur species apparently can cause iron disulfides to form directly on elemental sulfur grains (GOLDHABER & STANTON, 1987; SCHOONEN & BARNES, 1991a, b, c). Thus a local source of elemental sulfur in tube mucus can cause marcasite precipitation both by direct reaction with FeS precursors, or indirectly through the generation of intermediate sulfur species.

## DISCUSSION

The alvinellid worms (*Alvinella* spp. and *Paralvinella* spp.) probably evolved from a common ancestor that colonized the East Pacific Rise and the Juan de Fuca Ridge when they were contiguous (TUNNICLIFFE *et al.*, 1993). Since the separation of the two ridge systems some 25 million years ago, *Alvinella* spp. and *P. sulfincola* have probably evolved separately. *Alvinella* spp. is the more derived form; epidermal structures that accomodate epibiotic bacteria and organized tube ultrastructure are two examples of the specialized traits that have appeared in this genus. DESBRUYÈRES & LAUBIER (1991) propose an early separation of the genus *Alvinella* from evolutionary lines taken by the *Paralvinella* species.

The fact that *Paralvinella sulfincola* colonizes the same high temperature, high sulfide environment as *Alvinella* spp. raises questions about the importance of the *Alvinella* spp. epibiotic bacteria. *P. sulfincola* is able to enzymatically oxidise sulfide, as are many benthic polychaetes from non-vent environments. *Alvinella* spp. probably does the same, and the example of *P. sulfincola* indicates that this capability should be enough to allow the animal to survive and grow on sulfide chimneys. Then why the symbiosis? The elaborate adaptation of the epidermis to accomodate bacteria indicates that this is more than a simple case of epizooic growth of bacteria. Perhaps the symbiosis reduces the energetic cost of sulfide oxidation to animal. This may explain the larger body size of *Alvinella* spp. compared to *P. sulfincola*. Average wet weights for *A. caudata* and *A. pompejana* are 845 and 783 mg, respectively (TUNNICLIFFE, pers. comm.), whereas wet weights for *P. sulfincola* are around 325 mg (JUNIPER *et al.*, 1992).

The type of nutritional relationship between *Alvinella* spp. and its episymbionts first proposed by ALAYSE-DANET *et al.* (1986) has never been demonstrated in any other organism. Apart from an ability for DOM uptake by the epidermis of *Alvinella* spp., not uncommon among invertebrates, there is little evidence to support any transfer of metabolites from the epibiotic bacteria to the worm. On the other hand, there is good reason to suppose that *Alvinella* spp. and the sulfide worm are deposit feeders. Both worms are anatomically capable of deposit feeding and both are known to ingest particulates from their immediate environment. Without furthur evidence for symbiosis in *Alvinella* spp., deposit feeding remains its most likely mode nutrition. The fact that *P. sulfincola* is able to nourish itself in the same habitat without episymbionts further supports deposit feeding as the primary mode of *Alvinella* spp. nutrition. A similar grazing/detritivorous mode of nutrition appears to have been adopted by the Bresiliid shrimp on chimneys at Mid-Atlantic Ridge vents. In the absence of vent polychaetes, swarms of shrimp ingest mineral particles and adhering bacteria from the surfaces of black smoker chimneys (VAN DOVER *et al.* 1988; SEGONZAC, 1992).

The influence of *Alvinella* spp. on chimney mineralization has not been examined in the same detail as have the effects of *P. sulfincola*. From descriptions by HAYMON & KASTNER (1981) and DESBRUYÈRES *et al.* (1985), it would appear that *Alvinella* spp. influences chimney morphology to a greater degree than does *P. sulfincola*. In their account of the texture of black smoker chimney samples from East Pacific Rise vents, HAYMON and KASTNER (1981) note an abundance of interconnected cavities in the outer part of the chimney that are clearly remains of *Alvinella* spp. Another type of edifice, the white smokers or snow ball diffusers of EPR vents are referred to as biogenic edifices created by *Alvinella* spp. (FUSTEC *et al.*, 1987). No equivalent structures are known from northeast Pacific vents, even though the chemistry of the source fluids for edifice construction is similar (TUNNICLIFFE *et al.*, 1986; VON DAMM & BISCHOFF, 1988; BUTTERFIELD, 1990). How *Alvinella* spp. shapes chimney morphology is not known. One possible mechanism may involve the effect of convective circulation of cold seawater through the worm's U-shaped tube. *Alvinella* spp. contructs its tube so that the central portion of the tube is cemented against the chimney wall, with the anterior and posterior openings extending into the surounding seawater. This configuration allows a convective movement of seawater through the tube, that is driven by heat

Source : MNHN, Paris

flow into the tube from the chimney wall. Mineralogical studies of *Alvinella* spp. tubes indicate that convective cooling around the tubes locally reduces chimney wall temperatures enough to saturate metal-bearing fluids and cause mineral precipitation (DESBRUYÈRES *et al.*, 1985). This convectively driven "supercooling" extracts heat from the entire chimney structure. It may occasionally be of great enough magnitude to reduce temperatures deep inside the chimney wall, increasing local precipitation of minerals from high temperature fluids. This could increase outward accretion of chimney material at the expense of upward accretion, and cause some young chimneys to develop into snow ball structures. Whatever the mechanism, it is clear that *Alvinella* spp. is capable of a much greater degree of habitat modification than its counterpart at northeast Pacific vents, *Paralvinella sulfincola*. One notable difference between East Pacific Rise (EPR) and northeast Pacific vents is the relative rarity of vestimentiferans on chimneys at EPR. Is this a result of habitat modification by *Alvinella* spp ?

## CONCLUSION

While *P. sulfincola* and *Alvinella* spp. both exploit the high temperature chimney habitat of their respective spreading ridges, *Alvinella* spp. appears to be more elaborate in its adaptations to this environment. The functional significance of some of these adaptations remains to be clarified. *Alvinella* spp. may react to chimney growth by frequently abandoning tubes and migrating to new areas, as has been observed for *P. sulfincola*. Or, the more elaborate tube architecture and greater influence of *Alvinella* spp. on chimney morphology may be indicative of an organism that is better able to control its local microenvironment, and so reduce the frequency (compared to the sulfide worm) of tube abandonment. Time lapse photography was used to study tube building and migration of sulfide worms (JUNIPER *et al.*, 1992; TUNNICLIFFE *et al.*, 1993), and could probably be used to determine whether or not *Alvinella* spp. behaves similarly. In light of recent work on the effects of sulfide worms on chimney mineralization, the entire question of how *Alvinella* spp. influences chimney growth patterns needs reexamining. As well, this comparison has shown that the two roles proposed for the epibiotic bacteria in *Alvinella* spp., nutrition and detoxification, can be accomplished by *P. sulfincola* without the aid of episymbionts. This is a strong argument for a re-examination of the nature of the *Alvinella* -bacteria symbiosis.

## ACKNOWLEDGMENTS

Financial support for this work was provided by the NSERC Canada. Comments by Verena TUNNICLIFFE and Ian JONASSON were valuable in developing this manuscript. Daniel DESBRUYÈRES and an anonymous referee provided helpful reviews. Henriette GAGNON prepared the figures.

## REFERENCES

ALAYSE-DANET, A.-M., GAILL, F., & DESBRUYÈRES, D., 1986. — *In situ* bicarbonate uptake by bacteria- *Alvinella* associations. *Mar. Ecol.*, **7** : 233-240.

BAROSS, J.A. & DEMING, J.W., 1985. — The role of bacteria in the ecology of black-smoker environments. *In* : Hydrothermal Vents of the Eastern Pacific: An Overview. M.L. JONES (ed). *Biol. Soc. Wash. Bull.*, **6** : 355-371.

BAROSS, J.A., LILLEY, M.D. & GORDON, L.I., 1982. — Is the $CH_4$, $H_2$ and CO venting from submarine hydrothermal systems produced by thermophilic bacteria? *Nature* , **298** : 366-368.

BUTTERFIELD, D., 1990. — Geochemistry of hydrothermal fluids from Axial Seamount Hydrothermal Emissions Study vent field, Juan de Fuca Ridge: subseafloor boiling and subsequent fluid-rock interaction.. *J. Geophys. Res.*, **95** : 12,895-12,921.

CHEVALDONNÉ, P., DESBRUYÈRES, D. & CHILDRESS, J.J., 1992. — ... and some even hotter. *Nature*, **359** : 593-594.

DESBRUYÈRES, D., GAILL, F., LAUBIER L. & FOUQUET, Y. 1985. — Polychaetous annelids from hydrothermal vent ecosystems: An ecological overview. *Biol. Soc. Wash. Bull.*, **6** : 103-116.

DESBRUYÈRES, D., & LAUBIER, L., 1986. — Les Alvinellidae, une famille nouvelle d'annélides polychètes inféodées aux sources hydrothermales sous-marines : systématique, biologie et écologie. *Can J. Zool.*, **64** : 2227-2245.

DESBRUYÈRES, D., & LAUBIER, L., 1991. — Systematics, phylogeny, ecology and distribution of the Alvinellidae (Polychaeta) from deep-sea hydrothermal vents. *Ophelia* Suppl. **5** : 31-45.

FUSTEC, A., 1985. — *Microdistribution et variations temporelles de la faune hydrothermale des sites de la zone "13 °N" sur la Ride du Pacifique est.* Thèse, Docteur-Ingenieur. Université de Rennes, France.

Source : MNHN, Paris

FUSTEC, A., DESBRUYÈRES, D. & JUNIPER, S.K., 1987. — Deep-sea hydrothermal vent communities at 13 °N on the East Pacific Rise: Microdistribution and temporal variations. *Biol. Oceanogr.*, **4** : 121-164.

GAILL, F., DESBRUYÈRES, D. & LAUBIER, L., 1988. — Relationships between the "Pompeii Worms" and their epibiotic bacteria. *Oceanol. Acta*, Suppl. **8** : 147-154.

GAILL, F., & HUNT, S., 1986. — Tubes of deep sea hydrothermal vent worms *Riftia pachyptila* (Vestimentifera) and *Alvinella pompejana* (Annelida). *Mar. Ecol. Prog. Ser.*, **34** : 267-274.

GAILL, F., & HUNT, S., 1991. — The biology of annelid worms from high temperature hydrothermal vent regions. *Rev. Aquat. Sci.*, **4** : 107-137.

GOLDHABER, M.B. & STANTON, M.R., 1987. — Experimental formation of marcasite at 150-200° C: Implications for carbonate hosted Pb/Zn deposits (abstr.). *Geol. Soc. Amer. Abstr. Prog.*, **19** : 678.

HANNINGTON, M.D. & SCOTT, S.D., 1988. — Mineralogy and geochemistry of a hydrothermal silica-sulfide-sulfate spire in the caldera of Axial Seamount, Juan de Fuca Ridge. *Can. Mineral.*, **26** : 603-625.

HAYMON, R.M., 1983. — The growth history of hydrothermal black smoker chimneys. *Nature*, **301** 695-698.

HAYMON, R.M., & KASTNER, M., 1981. — Hot spring deposits on the East Pacific Rise at 21°N; preliminary description of mineralogy and genesis. *Earth Planet. Sci. Lett.*, **53** : 363-381.

HÉKINIAN, R. & FOUQUET, Y., 1985. — Volcanism and metallogenesis of axial and off-axial structures on the East Pacific Rise near 13° N. *Econ. Geol.*, **80** : 221-249.

HÉKINIAN, R., FRANCHETEAU, J., RENARD, V., BALLARD, R.D., CHOUKROUNE, P., CHEMINÉE, J.L., ALBARÈDE, J.,MINSTER, J.-F., CHARLOU, J.-L., MARTY, J.-F. & BOULÈGUE, J., 1983. — Intense hydrothermal activity at the rise axis of the East Pacific Rise near 13° N: submarine witnesses the growth of sulfide chimney. *Mar. Geophys. Res.*, **6** : 1-14.

JANNASCH, H.W. & MOTTL, M.J., 1985. — Geomicrobiology of deep-sea hydrothermal vents. *Science*, **229** : 717-725.

JUNIPER, S.K., JONASSON, I.R., TUNNICLIFFE, V. &SOUTHWARD, A., 1992. — Influence of a tube-building polychaete on hydrothermal chimney mineralization. *Geology*, **20** : 895-898.

JUNIPER, S.K., 1988. — Géochimie et écologie d'un microenvironnement hydrothermal : les sécrétions de mucus de *Paralvinella palmiformis*. *Oceanol. Acta*, vol. spéc. **8** : 167-172.

JUNIPER, S.K., THOMPSON, J.A.J., & CALVERT, S.E., 1986. — Accumulation of minerals and trace elements in biogenic mucus at hydrothermal vents. *Deep-Sea Res.*, **33** : 401-412.

JUNIPER, S.K., TUNNICLIFFE, V. & FONTAINE, A.R., 1988. — Biological influences on mineral deposition at deep-sea hydrothermal vents. *NOAA National Undersea Research Program Report* **88**-4 : 99-118.

LAUBIER, L., DESBRUYÈRES, D. & CHASSARD-BOUCHAUD, C., 1983. — Microanalytical evidence of sulfur accumulation in a polychaete from deep-sea hydrothermal vents. *Mar. Biol. Lett.*, **4** : 113-116.

MUROWCHICK, J.B., & BARNES, H.L., 1986. — Marcasite precipitation from hydrothermal solution. *Geochim. Cosmochim Acta*, **50** : 2615-2629.

PARADIS, S., JONASSON, I.R., LE CHEMINANT, G.M. & WATKINSON, D.H., 1988. — Two zinc-rich chimneys from the plume site, southern Juan de Fuca. *Can. Mineral.*, **26** : 637-654.

PLEDGER, R.J. & BAROSS, J.A., 1989. — Characterization of an extremely thermophilic Archaebacterium isolated from a black smoker polychaete (Paralvinella sp.) at the Juan de Fuca Ridge. *System. Appl. Microbiol.*, **12** : 249-256.

PLEDGER, R.J. & BAROSS, J.A., 1991. — Preliminary description and nutritional characterization of a chemoorganotrophic archaeobacterium growing at temperatures of up to 110 °C. *J. Gen. Microbiol.*, **137** : 203-211.

SAULNIER-MICHEL, C., GAILL, F., HILY, A., ALBÉRIC, P. & COSSON, M.-A., 1989. — Structure and functiopns of the digestive tract of *Alvinella pompejana*, a hydrothermal vent polychaete. *Can. J. Zool.*, **68** : 722-732.

SCHOONEN, M.A.A., & BARNES, H.L., 1991a. — Reactions forming pyrite and marcasite from solution: I. Nucleation of $FeS_2$ below 100°C. *Geochim. Cosmochima Acta*, **55** : 1495-1504.

SCHOONEN, M.A.A., & BARNES, H.L., 1991b. — Reactions forming pyrite and marcasite from solution: II. Via FeS precursors below 100 °C. *Geochim. Cosmochim. Acta*, **55** : 1505-1514.

SCHOONEN, M.A.A., & BARNES, H.L., 1991c. — Mechanisms of pyrite and marcasite formation from solution: III. Hydrothermal processes. *Geochim. Cosmochim. Acta*, **55** : 3491-3504.

SEGONZAC, M., 1992. — Les peuplements associés à l'hydrothermalisme océanique du Snake Pit (dorsale médio-atlantique: 23°N, 3 480m): composition et microdistribution de la mégafaune. *C.R. Acad. Sci. Paris*, **314**, sér.III : 593-600.

SOMERO, G.N., CHILDRESS, J.J. & ANDERSON, A.E., 1989. — Transport, metabolism and detoxification of hydrogen sulfide in animals from sulfide-rich marine environments. *Crit. Rev. Aquat. Sci.*, **1** : 591-614.

TIVEY, M.K. & DELANEY, J.R., 1986. — Growth of large sulfide structures on the Endeavour Segment of the Juan de Fuca Ridge. *Earth Planet. Sci. Lett.*, **77** : 303-317.

Source : MNHN, Paris

TIVEY, M.K., OLSON, L.O., MILLER, V.W. & LIGHT, R.D., 1990. — Temperature measurements during initiation and growth of a black smoker chimney. *Nature*, **346** : 51-54.

TUNNICLIFFE, V., BOTROS, M., de BURGH, M.E., DINET, A., JOHNSON, H.P., JUNIPER, S.K. & McDUFF, R.E., 1986. — Hydrothermal vents of Explorer Ridge, Northeast Pacific. *Deep-Sea Res.*, **33** : 401-412.

TUNNICLIFFE, V., DESBRUYÈRES, D., JOLIVET, D. & LAUBIER, L. 1993. — Systematic and ecological characteristics of *Paralvinella sulfincola* Desbruyères and Laubier, a new polychaete (family Alvinellidae) from northeast Pacific hydrothermal vents. *Can. J. Zool.*, **71** : 286-297.

TUNNICLIFFE, V., & JUNIPER, S.K., 1990. — Dynamic character of the hydrothermal vent habitat and the nature of the sulfide chimney fauna. *Prog. Oceanogr.*, **24** : 1-13.

VAN DOVER, C.L., FRY, B., HUMPRIS, S. & RONA, P.A., 1988. — Feeding biology of the shrimp *Rimicaris exoculata* at hydrothermal vents on the Mid-Atlantic Ridge. *Mar. Biol.*, **98** : 209-216.

VISMANN, B., 1990. — Sulfide detoxification and tolerance in *Nereis (Hediste) diversicolor* and *Nereis (Hediste) virens*. *Mar. Ecol. Prog. Ser.*, **59** : 229-238.

VON DAMM, K.L. & BISCHOFF, J.L., 1988. — Chemistry of hydrothermal solutions from the Southern Juan de Fuca Ridge. *J. Geophys. Res.*, **92** : 11, 334-11,346.

Source : MNHN, Paris

# Polychaete assemblages along a depth gradient in a Spitsbergen Fjord

*Michael A. KENDALL*

Plymouth Marine Laboratory
Prospect Place
Plymouth PL1 3DH, U.K.

ABSTRACT

Samples were taken at five depths in Sassenfjord, Spitsbergen (78°23'N - 16°23'E) during July 1990. Although essentially Arctic in character, this west coast fjord is also affected by the Atlantic water of the West Spitsbergen Current and both influences can be seen when one investigates the biogeographical affinities of the polychaete fauna. Diversity did not differ significantly from analogous sites previously sampled at lower latitudes. Polychaetes were numerical dominants at all stations and biomass dominants at all but one. The shallowest stations (30-95 m) appeared to be influenced by seasonal sediment deposition from an adjacent stream and could be shown to be in an intermediate state of disturbance. At these shallow sites the characteristic species were *Chaetozone setosa, Lumbrineris magnidenta, Tharyx sp.* indet., *Cossura longocirrata, Polycirrus arcticus* and *Chone duneri*. At the deepest site (123 m) the faunal composition of the assemblage changed considerably and the standing crop wet weight biomass increased to in excess of 100 g.m$^{-2}$. This substantial increase was largely due to four polychaete species, *Maldane sarsi, Spiochaetopterus typicus, Terebellides stroemi* and *Pectinaria hyperborea.*

RÉSUMÉ

**Assemblages annélidiens le long d'un gradient de profondeur dans un fjord du Spitzberg**

Des prélèvements ont été effectués à cinq profondeurs dans le Sassenfjord, Spitzberg (78°23'N - 16°23'E), en juillet 1990. Bien que de caractère essentiellement arctique, cette côte ouest du Spitzberg est aussi sous l'influence des eaux atlantiques du courant du Spitzberg occidental et les deux influences peuvent être constatées lorsqu'on étudie les affinités biogéographiques de la faune de polychètes. La diversité ne diffère pas sensiblement des sites analogues précédemment étudiés à des latitudes plus basses. Les polychètes étaient numériquement dominants dans toutes les stations et leur biomasse aussi, à l'exception d'une station. Les stations les moins profondes (30-95 m) apparaissaient être influencées saisonnièrement par les apports sédimentaires d'un courant adjacent et pourraient être considérées comme présentant un stade intermédiaire d'instabilité. Les espèces caractéristiques de ces sites peu profonds étaient *Chaetozone setosa, Lumbrineris magnidenta, Tharyx sp.* indet., *Cossura longocirrata, Polycirrus arcticus* and *Chone duneri*. A la station la plus profonde, la composition faunistique du peuplement était considérablement changée et la biomasse exprimée en poids humide était supérieure à 100 g. m$^{-2}$. Cet accroissement substantiel était essentiellement dû à quatre espèces de Polychètes, *Maldane sarsi, Spiochaetopterus typicus, Terebellides stroemi* et *Pectinaria hyperborea.*

KENDALL, M.A., 1994. — Polychaetes assemblages along a depth gradient in a Spitsbergen Fjord. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 463-470. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

A number of authors (ABELE & WALTERS, 1979 a, b; WARWICK & RUSWAHYUNI, 1987) have challenged SANDERS (1968) assertion that a gradient in macrobenthic diversity exists between the poles and the tropics. WARWICK & RUSWAHYUNI (1987) suggested that the issue should be re-addressed by the collection of new data sets which should be collected and analysed using fully standardised methods. To this end, they compared the diversity profiles of shallow sediments in Java and in the North Sea and showed no significant difference in a diversity between analogous sites in the two areas. The comparison has been extended to the fauna of Sassenfjord, Spitsbergen (78°N), by KENDALL & ASCHAN (1993) who were also unable to find differences between the three areas in the diversity of the infaunal macrobenthos.

At all of the stations studied in the Sassenfjord, polychaetes were the single most abundant phylum, but in the context of their paper, KENDALL & ASCHAN (1993) were unable to describe their pattern of distribution along the depth gradient which was sampled. One aim of this paper is to redress that shortcoming, as comparatively few data from such high latitudes exist and the comparison of those that do is fraught with difficulties resulting from methodological inconsistencies. In the context of the latitudinal diversity study referred to above, an attempt will be made to determine if the fauna of the area studied can be regarded truly representative of Arctic latitudes.

## MATERIAL AND METHODS

Five stations near Gipsvika, a bay in the Sassenfjord (west coast of Spitsbergen), were investigated. Stations will be referred to by their depth (Fig. 1). Samples were collected during July 1991 using a van Veen grab operated from the R.V. Johann Ruud. The sediment at the four shallowest stations was a silt with < 6 % sand, while at the 123 m station the silt contained 13 % sand. KENDALL & ASCHAN (1993) have used the ABC method of WARWICK (1986) to show that there is a disturbance gradient between the 30 m and 123 m sites.

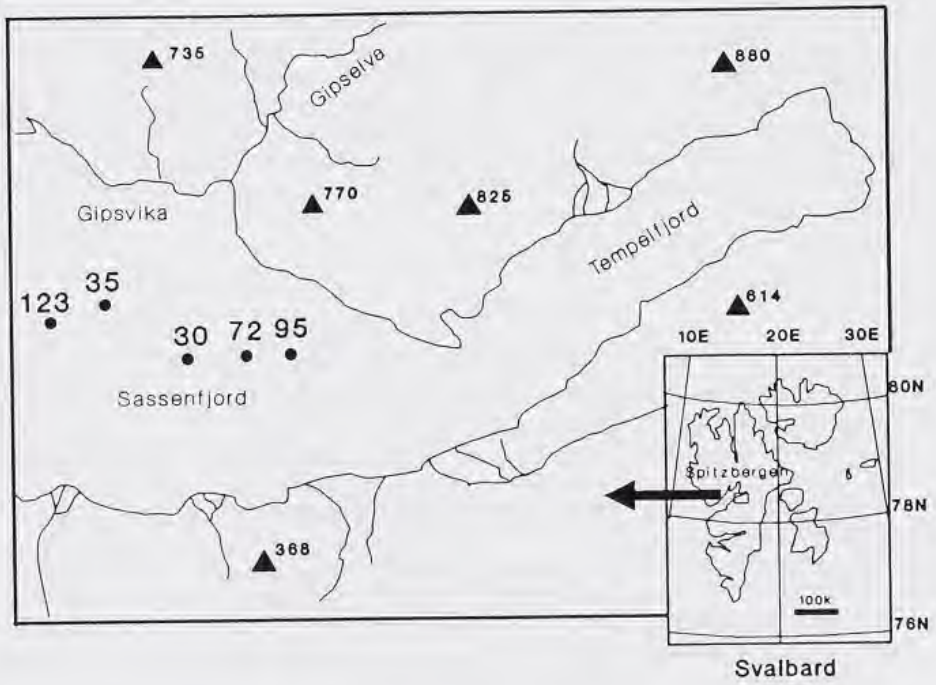



FIG. 1. — The location of the sampling sites in the Sassenfjord. The sites are referred to by their depth. The inset map of the Svalbard Archipelago indicates the position of Sassenfjord.

Source : MNHN, Paris

The fauna was extracted from each of the five replicates taken at each station by gently washing the sediment through a 0.5 mm square aperture sieve. The residue was fixed in formalin and preserved in 70 % ethanol. In the laboratory, all animals were extracted from the residual debris with the aid of a binocular microscope and were identified to putative species. Where possible, species have been named following HOWSON (1987). At all depths the samples contained large numbers of cirratulid polychaetes, many of which were damaged. For the purposes of community analyses the following genera have been grouped together: *Chaetozone, Caulleriella* and *Tharyx*. In many other cases complete identification has not yet been possible and so a full species list will not be presented in this paper, full details are available from the author. The blotted wet weight of each putative species was determined, as dry weighing destroys potentially valuable taxonomic material. Instead, dry weights have been estimated as 25 % of the wet weight (WARWICK & RUSWAHYUN, 1987). Species abundance data were subjected to non parametric multidimensional scaling (MDS analysis) using the Bray Curtis measure of similarity and group-average sorting after double square root transformation.

## RESULTS

COMMUNITY ANALYSIS. — MDS analysis of the data on taxa from all phyla shows a clear pattern which can be related both to depth and to sediment granulometry. All the replicates taken between 30 m and 95 m lie in order along the central axis of the plot (Fig. 2) with the shallowest sites at the top right-hand side and the deepest sites to the bottom left. This indicates a gradual change in the composition of the fauna with increasing depth The

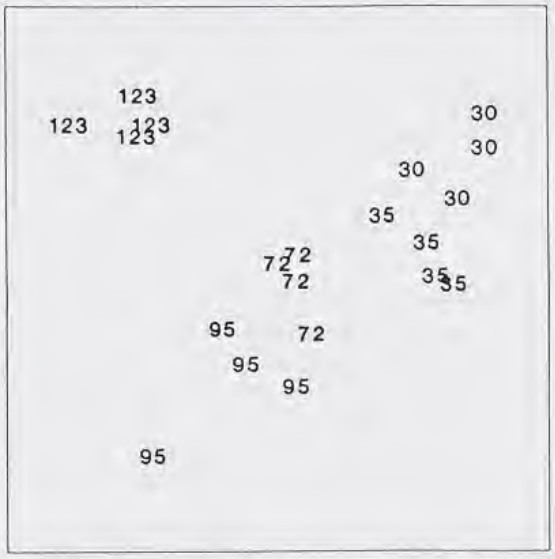



FIG. 2. — MDS plot comparing stations at different depths on the basis of all species present. Each replicate is plotted separately.

deepest station was clearly distinct from the shallower sites; on the MDS plot all replicates cluster together in the top left-hand corner. Figure 3 shows that at all depths annelids account for between 46 % and 59 % of all species and between 50 and 67 % of all individuals. Their contribution to the standing crop biomass is more variable (28 % at 73 m to 95 % at 123 m) but nevertheless they can be considered the dominant phylum.

PATTERNS IN ANNELID DISTRIBUTION. — Although there were 69 annelid taxa recorded, 14 of these account for 95 % of the individuals and 17 account for 95 % of the annelid biomass. The mean number of taxa per sample was greatest at the shallowest (30 m) site with a mean of 31 ± 3 (SD) but subsequently fell to between 23 and 24. No more than 36 annelid taxa were recorded in any single grab sample.

Source : MNHN, Paris

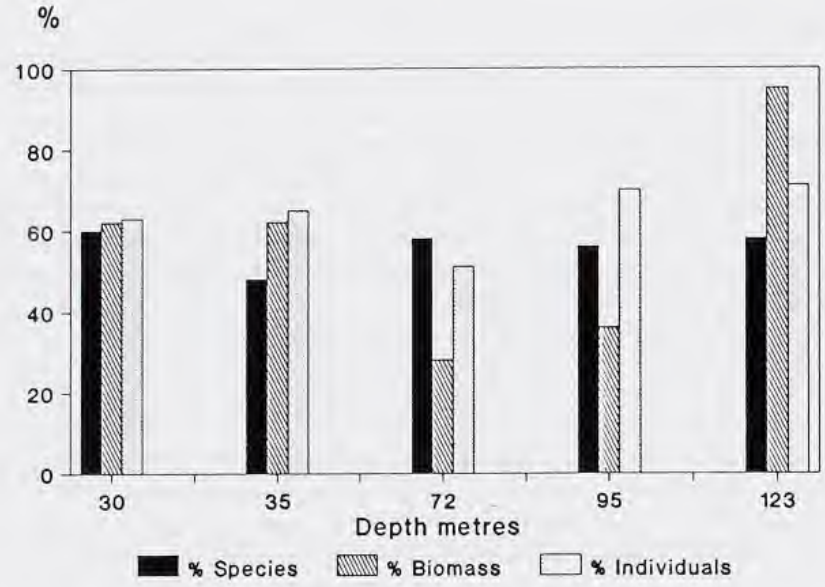



FIG. 3. — Bar histogram demonstrating the importance of polychaetes in the Sassenfjord assemblages.

MDS was used to cluster together species with similar patterns of distribution. For this analysis only the 14 most abundant species were considered. Figure 4 shows a major group of 10 species with four outliers. The two

MDS: Polychaete abundance

MDS: Polychaete biomass

FIG. 4 (left). — MDS plot comparing polychaete species in terms of their abundance at each depth. Key: Agl = *Aglophamus malmgreni*; Amp = *Ampharete finmarchica*; Api = *Apistobranchus tullbergii*; Aric= *Aricidea* indet.; Bin = B*rada inhabilis*; Bvi = *Brada villosa*; Cho = *Chone duneri*; Cir = Cirratulidae; Cos = *Cossura longocirrata*; Dorv = *Dorvillia rubrovittata*; Het = *Heteromastus filiformis*; Lao = *Laonice sarsi*; Lang = L*angerhansia cornuta*; Lev = *Levinsenia gracilis*; Lfr = *Lumbrineris fragilis*; Ltet = *Lumbrineris magnidenta*; Msar = *Maldane sarsi*; Nep = *Nephtys ciliata*; Pec = *Pectinaria hyperborea*; Pho= *Pholoe synopthalmica*; Phy = *Phyllodoce groenlandica*; Pol = *Polycirrus arcticus*; Sco = *Leitoscoloplos* indet.; Spc = *Spiochaetopterus typicus*; Tstr = *Terebellides stroemi*.

FIG. 5 (right) — MDS plot comparing polychaete species in terms of their biomass at each station. For key see Fig. 4.

Source : MNHN, Paris

species positioned above this group, *Pholoe synopthalmica* and *Aricidea* indet. are shallow water animals with poor penetration to greater depths. *Chone duneri* has a somewhat similar distribution but is more strongly represented below 35 m. The species lying to the right of the main group (*Dorvillia rubrovittata* and *Spiochaetopterus typicus*) are characteristic of deeper water. The remaining taxa were well represented at all depths but *Lumbrineris magnidenta*, the Cirratulidae, *Cossura longocirrata* and *Maldane sarsi* were particularly abundant at the 35 m station. In the latter case, most individuals at such shallow depths were small and immature. *Leitoscoloplos* indet. was evenly distributed between sites but *Terebellides stroemi* showed peaks in abundance at the shallowest and the deepest site. Once again, there was a substantial difference in the size of the animals with depth, the smallest individuals being at the shallowest sites.

A slightly different view of the assemblage emerges when one considers the distribution the various annelid species in terms of their biomass rather than their abundance. Only the 17 species accounting for 95% of the total biomass were included in the analysis. While many species which were considered important on the basis of abundance remain for consideration, they are joined by others which are larger but less common. In the MDS plot based on biomass data (Fig. 5) there is a central grouping of species having a broad depth distribution. This bears similarities to central grouping of the abundance plot (Fig. 4) as it contains the cirratulids, *Lumbrineris magnidenta, Maldane sarsi, Terebellides stroemi* and *Leitoscoloplos* indet. Above this group lie *Laonice sarsi* and *Polycirrus arcticus*; the first of these was best represented at 72 m while the latter was numerous at the 35 m station. Below the central grouping in Fig. 5 lie species which were characteristic of the 123 m site; *Pectinaria hyperborea, Spiochaetopterus typicus* and *Terebellides stroemi* At this depth polychaetes account for 95 % of the mean community wet weight biomass ($101 \pm 3$ g. $m^{-2}$) and the greatest part of this is due to these three species plus large individuals of *Maldane sarsi*. The remaining species in this grouping, *Phyllodoce groenlandica* occurred throughout the depth range but at shallower sites it was only represented by small individuals. Around the clusters which have already been discussed lies an arc of species which are included in the analysis by virtue of their large body size but, as they are comparatively rare, were not efficiently sampled by the sampling strategy which we employed; little importance can be attached to their distribution on the MDS plot. This group is composed of *Aglophamus malmgreni, Nephtys ciliata, Lumbrineris fragilis*, an unidentified species of *Euclymene, Brada villosa* and *B. inhabilis*.

## DISCUSSION

The benthic fauna of muddy sediments in Sassenfjord undergoes a gradual change in composition between 30 m and 93 m but before 123 m there is a clear transition from a moderately diverse community of animals of small body size, to an assemblage which has a high standing crop biomass and is dominated by large polychaetes. This does not appear to be a simple function of depth alone. Sassenfjord lies more than 70 km from the open sea and is ice-covered for much of the year; wave-induced disturbance is unlikely to be significant at any but the most shallow of sites. As KENDALL & ASCHAN (1993) have pointed out, it is more likely that the intensity of sediment deposition from the Gipselva stream will vary with distance from its outflow and with depth and so influence the benthic fauna. A similar situation is described in the Hornsund Fjord in the south of Spitsbergen by GORLISH *et al.* (1987) who suggest that the high rate of sediment deposition close to a glacier dilutes any available organic matter with indigestible material. This condition is exacerbated by low levels of bioturbation in the sediment and low primary production in the turbid water column. As the rate of sediment deposition decreases and bioturbation increases so does the abundance of benthic life. In such situations in the Canadian Arctic, SYVITSKI *et al.* (1989) have described a transition from a shallow assemblage dominated by the bivalve *Yoldiella* to a deeper assemblage characterised by *Maldane sarsi*; such a sequence was observed in the Sassenfjord.

In surveys around Raudfjord (N. Spitsbergen) and van Mijen Fjord (W. Spitsbergen), GULLISKEN *et al.* (1985) found the most abundant fauna outside the fjords with a decrease towards the innermost transects where they recorded no more than 8-10 species of all phyla in each 0.1 $m^2$ sample. They attribute this impoverishment to high levels of siltation and poor water exchange. Direct comparison with studies such as this and that of GORLISH *et al.* (1987), is difficult as the sampling methods used were not consistent; while GULLISKEN *et al.* (1985) separated the fauna from the sediment using a 1 mm mesh, GORLISH *et al.* (1987) employed one of 2 mm. It is equally difficult to be sure how the results of their analyses compare with those of the Sassenfjord study. While the larger meshes would tend to underestimate the abundance of species with small body size, there would be little difference in estimates of biomass. Nevertheless, it seems that the Sassenfjord fauna might be unusually rich as GULLISKEN *et al.* (1985) record diversity values similar to those which have been calculated in the present study,

Source : MNHN, Paris

despite the probability that they underestimated the abundance of the smallest individuals. WESLAWSKI *et al.* (1990) consider the area unusually rich in comparison with other Spitsbergen fjords. Although the sampling sites in Sassenfjord were clearly under the influence of suspended matter deposited by the Gipselva stream, if the conditions described by WESLAWSKI *et al.* (1990) are typical (Secchi disc depths of 3-8 m) then it is unlikely that the sedimentation regime is as severe as in the other fjords. It is also possible that local upwelling (WESLAWSKI *et al.*, 1990) may stimulate primary production in the water column to levels greater than those elsewhere in Spitsbergen. Such intermediate levels of disturbance accord well with the ABC plots of KENDALL & ASCHAN (1993) and may well account for the high diversity of this area.

SANDERS (1968) claimed that there was a polar-tropical gradient in the macrobenthic fauna of soft sediments. When the fauna of the 123 m site in Sassenfjord was compared with a similarly disturbed offshore sandy mud in the North Sea, using directly comparable methods, little difference could be observed in their a-diversity profiles (KENDALL & ASCHAN, 1993). The polychaete component of the infauna of the two areas was broadly similar, both in the number of species and in wet weight biomass, although at the Arctic site the mean density of individuals was higher (KENDALL, unpublished). These observations support THORSON's (1957) assertion that the infauna does not show the same degree of latitudinal variability as the epifauna. However, such an inference assumes that both of the locations have a faunal diversity which is typical of their latitude. While there is no cause to question the representativeness of the North Sea site, it is not clear just how well Sassenfjord represents Arctic conditions. Certainly, physical data suggest that the area is a good example: at 78°N the sun is below the horizon from the start of November until the end of February, fjords are ice-covered from 6-10 months of the year (EILERSTSEN *et al.*, 1989) and in the Sassenfjord itself the bottom temperature during summer is less than 0.5 °C (WESLAWSKI *et al.*, 1990). On the other hand, faunal evidence suggests that the area is not fully Arctic.

While the composition of the Sassenfjord fauna shows strong Arctic influences, boreal and/or cosmopolitan polychaete species appear to be disproportionately important when their contribution to the total abundance or biomass is considered. Many of the species sampled in the Sassenfjord are also commonly recorded in the North Sea (*cf.* BUCHANAN & MOORE, 1986) This confirms a finding from other fjords on the north and west coasts of Spitsbergen (GULLISKEN *et al.*, 1985). In reporting their study they claim that all the polychaetes they encountered were recorded from both Arctic and boreal waters. STROMBERG (1989) too records the importance of boreal species in this area and attributes their importance to the influence of the Atlantic water of the northern-flowing West Spitsbergen Current. In the Beaufort Sea (71°N), BILYARD & CAREY (1980) have also observed substantial numbers of non-endemic species in water shallower than 300m, but rather than attributing their presence to warming currents they relate their presence to inter-glacial invasions. The real extent of this boreal intrusion into Spitsbergen waters may not, however, be as great as the data immediately suggest. The status of a number of the more important boreal, or cosmopolitan species of the area has been questioned in recent years; among these are *Terebellides stroemi* (WILLIAMS, 1984), *Tharyx* (BLAKE, 1991), *Chaetozone* (CHRISTIE, 1985), *Cossura longocirrata* (FOURNIER & PETERSEN, 1991) while LIGHT (1991) lists four sub-species of *Maldane sarsi*. It is possible that other "species" with very broad ranges might similarly prove to be complexes of sibling species. It is unlikely that the existence of a substantial proportion of non-endemic species in Sassenfjord is in any way unusual for a shallow water Arctic assemblage.

ZENKEVITCH (1963) recognised six major macrofaunal assemblages in the adjacent Barents Sea and none of these had the faunal characteristics recorded in Sassenfjord. In a broad scale study of the Arctic Chukchi Sea and the sub-Arctic Bering Sea, GREBMAIER *et al.*, (1989) have described 11 different assemblages which vary substantially in the identity of the dominant phylum. In doing so, they demonstrated the relationship between the properties of the sediment and the community it supports. Nevertheless, the most northerly mud community which was described, and hence that which was most comparable to that in Sassenfjord, was clearly dominated by amphipods rather than by polychaetes. This serves to emphasise the potential for variation in the structure of Arctic assemblages and so brings the present study into perspective. The comparison between an Arctic site and analogous sites in the North Sea and Java (KENDALL & ASCHAN, 1993) has shown few differences in the a-diversity of either the whole community or the polychaete component of it. On the basis of such a limited comparison it would be unrealistically hasty to dismiss existing hypotheses concerning latitudinal variability in patterns of infaunal diversity. Even in a study in which an effort is made to hold variables such as sediment type and depth as constant as possible, we must expect to encounter a variety of communities each of which will have its own diversity properties. As yet we cannot be sure of the position of the Sassenfjord sites within such a range. For this reason, if we are to address the problem of latitudinal patterns of diversity we must first establish the range of variation within the areas which we are comparing.

Source : MNHN, Paris

## ACKNOWLEDGEMENTS

I would like to thank Michaela ASCHAN of the University of Tromsö for arranging my visit to Spitsbergen, and Dr R.M.WARWICK for his comments on the mânuscript.

## REFERENCES

ABELE, L.G. & WALTERS, K., 1979a. — The stability-time hypothesis: reevaluation of the data. *Am. Nat.*, **114** : 559-568.

ABELE, L.G. & WALTERS, K.,1979b. — Marine benthic diversity: a critique and alternative explanation. *J. Biogeogr.* **6** : 115-126.

BILYARD, G.R. & CAREY Jr., A.G., 1980. — Zoogeography of western Beaufort Sea Polychaeta (Annelida). *Sarsia*, **65** : 19-26.

BLAKE, J.A.1991. — Revision of some genera and species of Cirratulidae (Polychaeta) from the western North Atlantic. *Ophelia*, suppl. **5** : 17-30.

BUCHANAN, J.B. & MOORE, J.J., 1986. — Long-term studies at a benthic station off the coast of Northumberland. *Hydrobiologia*, **142** : 121-127.

CHRISTIE, G. 1985. — A comparative study of the reproductive cycles of three Northumberland populations of *Chaetozone setosa* (Polychaeta: Cirratulidae). *J.mar. biol. Ass. U.K*, **65** : 239-254.

EILERTSEN, H.C., TAASEN, J.M. & WESLAWSKI, J.P., 1989. — Phytoplankton Studies in the fjords of West Spitsbergen: physical environment and production in spring & summer. *J. Plankton Res.*, **11** : 1245-1260.

FOURNIER J.A. & PETERSEN, M.E., 1991. — *Cossura longocirrata:* Redescription and distribution, with notes on reproductive biology and a comparison of described species of *Cossura* (Polychaeta: Cossuridae). *Ophelia*, suppl. **5** : 63-80.

GORLICH, K., WESLAWSKII, J.M. & ZAJACKOWSKI, M., 1987. — Suspension settling effect on macrobenthos biomass distribution in the Hornsund Fjord, Spitsbergen. *Polar Research* , **5** : 175-192.

GREBMEIER, J.M., FEDER, H.M. & MCROY, C.P., 1989. — Pelagic benthic coupling on the shelf of the northern Bering and Chukchi Seas. II Benthic community structure. *Mar. Ecol. Prog. Ser.*, **51** : 253-268.

GULLIKSEN B., HOLTE, B. & JAKOLA, K-J., 1985. — The soft bottom fauna in van Mijenfjord and Raudfjord, Svalbard. *In* : J.S.GRAY & M.E.CHRISTIANSEN (eds), *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*. John Wiley & Sons :199-211.

HOWSON, C., 1987. — *Directory of the British marine fauna and flora. A coded checklist of the marine flora and fauna of the British Isles and its surrounding seas*. Marine Conservation Society, Ross on Wye, 471 pp.

KENDALL, M.A. & ASCHAN, M., 1993. — Latitudinal gradients in the structure of macrobenthic communities: a comparison of Arctic temperate and tropical sites. *J. exp. mar. Biol. Ecol.*, **172** : 157-169.

LIGHT, W.J.H., 1991. — Systematic revision of the genera of the polychaete subfamily Maldanidae Arwidsson. *Ophelia*, suppl. **5** : 133-146.

SANDERS, H.L., 1968. — Marine benthic diversity : a comparative study. *Am. Nat.*, **102** : 243-282.

STROMBERG, J-O., 1989. — Northern Svalbard waters. *In* : L. REY, L. and V. ALEXANDER (eds), *Proceedings of the 6th Comité Arctique International*, 13- 15 May 1985. Brill, Leiden : 402-426.

SYVITSKI, J.P.M., FARROW, G.E., ATKINSON, R.J.A., MOORE, P.G. & ANDREWS, J.T., 1989. — Baffin Island Fjord Macrobenthos: Bottom Communities and Environmental Significance. *Arctic*, **42** : 232-247.

THORSON, G. 1957 — Bottom communities (sublittoral or shallow shelf). *In* : J.W. HEDGPETH (ed.), *Treatise on marine ecology and paleoecology*, Geological Society of America: New York : 461-534.

WARWICK R.M., 1986. — A new method for detecting pollution effects on marine macrobenthic communities. *Mar. Biol.*, **92** : 557-562.

WARWICK, R.M. & RUSWAHYUNI, R.M., 1987. — Comparative study of the structure of some tropical and temperate marine soft bottom macrobenthic communities. *Mar. Biol.*, **95** : 641-649.

Source : MNHN, Paris

WESLAWSKI, J.M., WASNIEWSKI, S.K., S.SWERPWL, S., WICTOR, J., AJACZKOWSKI, M., OSTROWSKI, M. & SIWECKI, R., 1990. — Summer environmental survey of Gipsvika, Svalbard. *Norsk Polarinstitutt Rapport*, **62** : 111-131.

WILLIAMS, S.J., 1984. — The status of *Terebellides stroemi* (Polychaeta Trichobranchidae) as a cosmopolitan species based on a world-wide morphological survey including descriptions of two new species. *In*: P.A. HUTCHINGS (ed.), *Proceedings of the First International Polychaete Conference*, Sydney. Linnean Society of New South Wales : 118-142.

ZENKEVITCH, L., 1963. — *The Biology of the Seas of the U.S.S.R.* George Allen & Unwin Ltd. London, 955 pp.

Source : MNHN, Paris

# The biogeography of some abyssal Polychaetes

*Jørgen B. KIRKEGAARD*

Zoological Museum, Universitetsparken 15
K–2100 Copenhagen, Denmark

ABSTRACT

The Danish Galathea Expedition obtained polychaetes from 83 stations in the bathyal and abyssal zones of the South Atlantic, Indian, and southern Pacific Oceans; 104 species were identified. On the basis of the distribution of some of these species and results from earlier publications a biogeographical analysis is given. The species treated in detail were: *Laetmonice benthaliana* McIntosh, *Leanira quatrefagesi* Kinberg, *Aglaophamus elamellata* Eliason, *Bathyeliasona kirkegaardi* (Uschakov), *B. nigra* (Hartman) and *Paradiopatra paucibranchis* (Ehlers). This analysis showed a worldwide distribution of many abyssal polychaetes. The abyssal and hadal polychaetes are derived from the polychaete fauna in the bathyal zone. Many of these species were eliminated during the glacial ages when temperatures in the deep sea dropped from 10 °C to 2 °C. The present deep–sea polychaete fauna consists of eurythermic and eurybathic species, relics of a preglacial fauna, and new invaders from the bathyal zone.

RÉSUMÉ

**Biogéographie de quelques Polychètes abyssaux**

L'expédition danoise de la "Galathea" a récolté des polychètes dans 83 stations, dans les zones bathyale et abyssale de l'Atlantique du Sud, de l'Océan Indien et du Pacifique du Sud. Cent quatre espèces ont été identifiées. Il est fourni, sur la base de la distribution de quelques unes de ces espèces et de résultats antérieurs, une analyse biogéographique. Les espèces suivantes ont été étudiées en détail : *Laetmonice benthaliana* McIntosh, *Leanira quatrefagesi* Kinberg, *Aglaophamus elamellata* Eliason, *Bathyeliasona kirkegaardi* (Uschakov), *B. nigra* (Hartman) et *Paradiopatra paucibranchis* (Ehlers). Les polychètes abyssaux et hadaux dérivent de la faune de polychètes de la zone bathyale. Plusieurs de ces espèces ont disparu au cours des périodes glaciaires, quand les températures dans l'océan profond baissaient de 10 °C à 2 °C. Il en résulte que la faune actuelle de polychètes de l'océan profond se compose d'espèces eurythermes et eurybathes, des restes d'une faune pré-glaciaire, et de nouveaux envahisseurs de la zone bathyale.

## INTRODUCTION

The polychaetes have long been considered to be a group with many cosmopolitan species. In recent years polychaete specialists have reexamined so–called cosmopolitan species resulting in revision of genera and species

KIRKEGAARD, J.B., 1994.— The biogeography of some abyssal Polychaetes. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 471-477. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

in many families. This has shown that in many cases the purportedly cosmopolitan distribution in the oceans was due to inadequate descriptions or lack of comparison with type specimens. As a result many of the so–called cosmopolitan species have been split up into several species with a more restricted distribution. However, this is probably not true of polychaetes living in the deep sea.

## DEEP–SEA POLYCHAETES

Before 1940 little was known about the deep–sea fauna. Our knowledge of the deep–sea polychaetes was based mostly on the investigation of the "Challenger" expedition (MCINTOSH, 1885). Since the late 1940s several expeditions have investigated deep-sea fauna with research vessels such as the Swedish "Albatross", the Danish "Galathea", the Soviet "Vitiaz" and the American "Anton Bruun". Later, British, German, French, and Japanese research vessels sampled bathyal, abyssal and hadal bottoms. We now have more detailed knowledge of the polychaete fauna of the deep sea, however, since more than half of the world's oceans is occupied by the abyss, only a small part has been sampled.

The Danish "Galathea" expedition round the world in 1950–52 collected polychaetes from 97 deep-sea stations. These stations were situated in the Southeast Atlantic, the Indian Ocean and the South Pacific. Fourteen of the stations were located in trenches deeper than 6,000 m, the so–called hadal region, from which 15 species were obtained (KIRKEGAARD, 1956). The remaining 83 stations were from the abyssal (43) and bathyal (40) regions. The errant species from these 83 stations have been identified and comprise 104 species from 17 families (KIRKEGAARD, in prep.). These species were obtained using several different gears, including sledge trawls, commercial trawls, dredges, and Petersen grab. The material was washed through sieves of different mesh size, the smallest with a mesh of 1 mm. However, the results from this expedition and from other expeditions (LEVENSTEIN, 1962, 1971, 1975, 1978a, b, 1984, 1991; USCHAKOV, 1955) make it possible to draw some conclusions on the biogeography of deep–sea polychaetes.

The abyssal plains stretch from south of Greenland southwards through the Atlantic, south of Africa to the Indian Ocean, south of Australia and into the Pacific. These plains occupy the bottom of nearly all of the large oceans, 273 million km$^2$. The conditions for life are similar throughout these large areas: 2–4 °C, 35 P.S.U. salinity, oxygen: 4 ml. l$^{-1}$ pressure: 200-600 atm., and darkness (BRUUN, 1956). It is on these large areas with similar conditions for life from one ocean to another that cosmopolitan species, if they exist, might be expected to occur.

## RESULTS

### *Laetmonice benthaliana* McIntosh, 1885

(DAY, 1967, fig. 1.1 f–l) Fig. 1.

RECORDS. — *Laetmonice producta* var. *benthaliana* McIntosh, 1885 p. 45 pl. 8, figs 4–5, pl. 4A, fig. 12, pl. 5A figs 1–2. — *Laetmonice producta benthaliana* HARTMAN, 1964 p. 12, pl. 1 figs 4–5. — *Laetmonice benthaliana* USCHAKOV, 1962 p. 147; DAY, 1963 p. 356, 1967 p. 33.

MATERIAL EXAMINED. — St. 186, SE of Natal, 32°33'S, 32°01'E, 3620 m, SOT, two specimens: 50 x 20 mm (complete, 34 setigers), 50 x 20 mm (bad condition). St. 192, off Durban, 32°00'S, 32°41'E, 3,530 m, SOT, five complete specimens, 34 setigers: 20 x 5, 35 x 15, 40 x 15, 45 x 15, 45 x 20 mm; one destroyed specimen. St. 198, off Durban, 30°32'S, 34°27'E, 2,700 m, ST100, one complete specimen, 34 setigers: 34 x 12 mm. St. 217, Mozambique Channel, 14°20'S, 45°09'E, 3,390 m, HOT, one complete specimen, 34 setigers: 40 x 15 mm. St. 233, N of Madagascar, 7°24'S, 48°24'E, 4,720 m, ST300, one specimen, 34 setigers: 55 x 20 mm. St. 235, E of Mombasa, 4°47'S 46°19'E, 4,810 m, HOT, 1 specimen, 34 setigers: 60x15 mm. St. 238, off Kenya, 3°23'S, 44°04'E, 3,960 m, 43 specimens: 50 x 20 mm. St. 241, off Kenya, 4°00'S, 41°27'E, 1,510 m, HOT, one specimen: 10 x 5 mm (smashed). St. 601, SW of New Zealand, 45°51'S, 164°32'E, 4,400 m, HOT, seven complete specimens, 34 setigers: 35 x 10–45 x 15 mm, three fragments: 20 x 8–40 x 15 mm. St. 607, SW of New Zealand, 44°18'S, 166°46'E, 3,580 m, HOT, 10 specimens, 34 setigers: 10 x 5–33 x 15 mm. St. 661, Kermadec Trench, 36°07'S, 178°32'W, 5340 m, ST600, three complete specimens: 23 x 10, 30 x 12, 35 x 12 mm. St. 663, Kermadec Trench, 36°31'S, 178°38'W, 4,410 m, HOT, 181 specimens 33–34 setigers: 35 x 10–15 x 5 mm. St. 664,

Source : MNHN, Paris

Kermadec Trench, 36°34'S, 178°57'W, 4,540 m, HOT, 76 specimens, many destroyed: 35 x 12 mm. St. 665, Kermadec Trench, 36°38'S, 178°21'E, 2,470 m, HOT, three complete specimens: 20 x 10, 20 x 10, 25 x 12 mm; one fragment. St. 716, Gulf of Panama, 9°23'N, 89°32'W, 3,570 m, HOT, one specimen: 30 x 10 mm.

REMARKS. — This species was originally described as a subspecies of *Laetmonice producta* by McINTOSH (1885). USCHAKOV (1962) raised it to species level and DAY (1963) agreed. It differs from the stem species by its smooth venter and by always having 15 pairs of elytra compared to 18–20 pairs in *L. producta*. The number of setigers is also smaller, 33–34 in *L. benthaliana* , 45–47 in *L. producta*.

DISTRIBUTION. — Antarctic; Indian Ocean, E and S of Africa, Ambian Sea, S of Ceylon; Pacific, W of New Zealand, Kermadec Trench, Japan, Central Pacific, Gulf of Panama. 50–6,875 m.

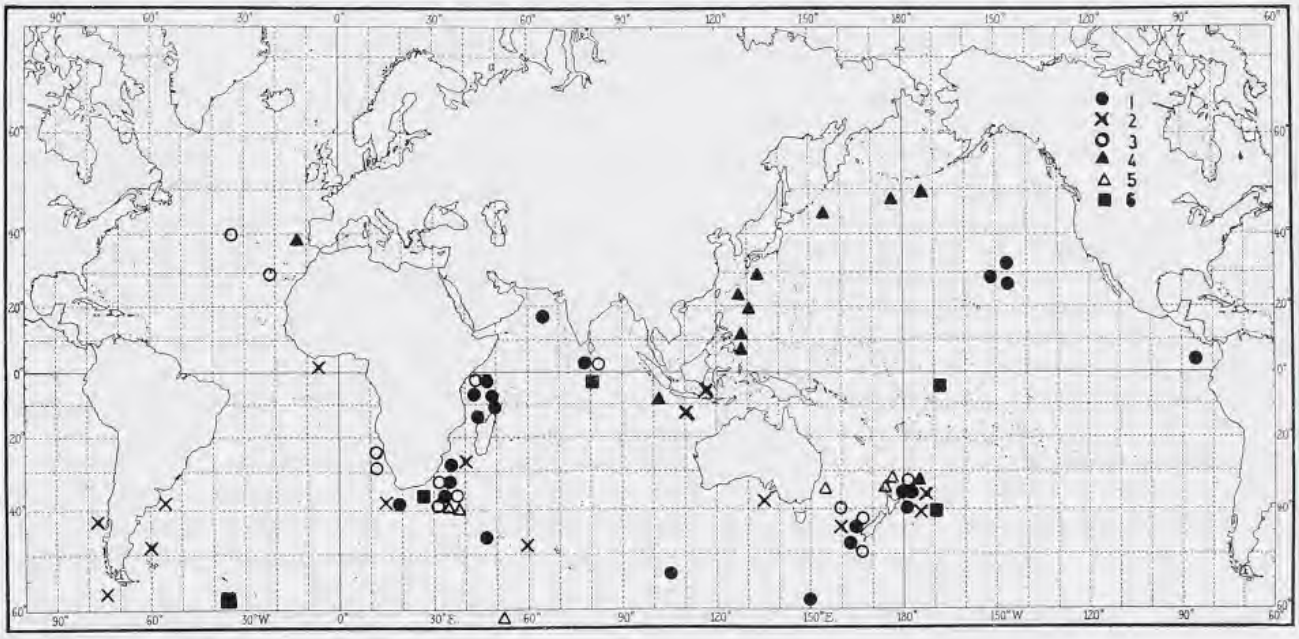



FIG. 1.— Distribution of *Laetmonice benthaliana* (1), *Leanira quatrefagesi* (2), *Aglaophamus elamellata* (3), *Bathyeliasona kirkegaardi* (4), *Paradiopatra paucibranchis* (5), and *Bathyeliasona nigra* (6).

## *Leanira quatrefagesi* Kinberg, 1855

(PETTIBONE, 1970, figs 1–3), Fig. 1.

RECORDS. — PETTIBONE, 1970 p. 4; WESENBERG-LUND, 1962, p. 27. *Leanira hystricis* DAY, 1963, p. 360.

MATERIAL. — St. 214, off Beira, 20°12'S, 35°15'E, 380 m, PG 0,2, one specimen: 25 x 5 mm (anterior end). St. 443, Mindanao Sea, 8°48'N, 124°09'E, 1,500 m, ST300, three specimens: 32 x 7, 30 x 8, 22 x 6 mm (anterior end). St. 453, Makassar Strait, 3°56'S, 118°26'E, 2,000 m, ST300, one specimen: 45 x 4 mm. St. 480, S of Bali, 8°49'S 115°00'E, 440 m, PG 0,2, one specimen: 8 x 0.5 mm (anterior end). St.491, Makassar Strait, 4°56'S, 117°39'E, 1,560 m, ST300, one specimen: 22 x 4 mm (anterior end), one fragment. St. 554, Great Australian Bight, 37°28'S, 138°55'E, 1,340–1,320 m, ST300, 16 specimens: 33 x 1–9 x 0.5 mm (anterior ends). St. 626, W of New Zealand, 42°10'S, 170°10'E, 610 m, HOT, 10 specimens: 22 x 1–5 x 1 mm (anterior ends), two posterior

Source : MNHN, Paris

ends, three fragments. St. 665, Kermadec Trench, 36°38'S, 178°21'E, 2,470 m, HOT, 13 specimens: 32 x 6–12 x 1 mm (anterior ends), eight fragments. ? St. 668, Kermadec Trench, 36°23'S, 177°41'E, 2640 m, HOT, one fragment (only parapodia with setae).

REMARKS. — This fairly large number of specimens from different parts of the world agrees with Pettibone's description and figures.

DISTRIBUTION. — South Atlantic off Argentina, West and South Africa, Indian Ocean off Mozambique, Malaya Archipelago, Pacific off Chile, W of New Zealand, Kermadec Trench, Magellan area, Falkland Islands, Antarctic. 0-6,150 m.

## *Aglaophamus elamellata* (Eliason, 1951)

(ELIASON, 1951, fig. 2), Fig. 1.

RECORDS. — *Nephthys elamellata* Eliason, 1951, p. 133; KIRKEGAARD, 1956, p. 68 fig. 7.

MATERIAL. — St. 101, off Angola, 8°50'S 12°32'E, 990 m, ST300, two specimens: 20 x 2 mm (anterior ends). St. 108, off Lobito, Angola, 12°00'S 13°00'E, 1,470 m, one specimen: 20 x 2 mm (anterior end). St. 192, off Durban, 32°00'S, 32°41'E, 3,430 m, ST100, one specimen: 20 x 3 mm (anterior end). St. 193, off Durban, 32°34'S 31°52'E, 3,680 m, SOT, 4 specimens: 22 x 3, 10 x 4, 6 x 2, 3 x 2 mm (anterior ends). St. 194, off Durban, 34°09'S 30°45'E, 4,360 m, SOT, three specimens: 25 x 2, 18 x 2, 5 x 2 mm (anterior ends). St. 241, off Kenya, 4°00'S, 41°27'E, 1,510 m, HOT, one specimen: 10 x 2 mm (anterior end). St.279, SW of Ceylon, 1°00'N, 76°17'E, 4,320 m, one specimen: 5 x 0.5 mm (complete), juvenile? St. 574, Tasman Sea, 39°45'S 159°39'E, 4,670 m, ST600, one specimen: 22 x 4 mm (anterior end). St. 601, W of New Zealand, 45°51'S 164°32'E, 4,400 m, HOT, three specimens: 25 x 5, 16 x 5, 20 x 5 mm. St. 607, off SW New Zealand, 44°18'S; 166°46'E, 3,830 m, VG 0.2, four specimens: 15 x 3, 15 x 3, 15 x 3, 10 x 2 mm (anterior ends). St. 654, Kermadec Trench, 32°10'S 175°54'W, 5,850–5,900 m, HOT, two specimens: 40 x 5, 38 x 5 mm (complete, 54 setigers). St. 663, Kermadec Trench, 36°31'S 178°38'W, 4,410 m, HOT, 18 specimens: 40–10 x 5 mm (anterior ends). St. 664, Kermadec Trench, 36°34'S, 178°57'W, 4,540 m, HOT, one specimen: 15 x 3 mm.

REMARKS. — This species was described from specimens found in the Central Atlantic. It was later recorded by me (KIRKEGAARD, 1956) from the bottom of the Kermadec Trench. The present records are from many intervening places and from other stations in the Kermadec Trench. I can find no differences between the Atlantic specimens and those from deep water in the Indian Ocean and around New Zealand. It appears that this is a deep water species with a cosmopolitan distribution.

DISTRIBUTION. — Atlantic (Azores, Canary Islands, off West Africa). 990–4,600 m. Indian Ocean (off East Africa, Ceylon). 1,510–4,360 m. Pacific (Tasman Sea, Kermadec Trench). 3,830–7,000 m.

## *Bathyeliasona kirkegaardi* (Uschakov, 1971)

(PETTIBONE, 1976, figs 15–17), Fig. 1.

RECORDS. — USCHAKOV, 1971, p. 37; PETTIBONE, 1976, p. 27; HARTMANN-SCHRÖDER, 1975, p. 53. *Macellicephala abyssicola* KIRKEGAARD, 1956, p. 64.

MATERIAL. — St. 654, Kermadec Trench, 32°10'S, 175°54'W, 5,850–5,900 m, HOT, two fragments, two proboscises.

REMARKS. — The species was identified by the setae on an anterior and a posterior end

DISTRIBUTION. — Aleutian Trench, Kermadec Trench, Sunda Trench, off Portugal. 5275–7880 m.

Source : MNHN, Paris

### *Bathyeliasona nigra* (Hartman, 1967)

(PETTIBONE, 1976, figs 18–19), Fig. 1.

RECORDS. — PETTIBONE, 1976, p. 30. *Herdmanella nigra* Hartman, 1967, p. 25.

MATERIAL. — St. 194, off Durban, 34°09'S, 30°45'E, 4,360 m, SOT, one specimen: 40 x 20 mm. St. 281, SW of Ceylon, 3°38'N, 78°15'E, 3,310 m, ST300, one specimen: 35 x 10 mm.

REMARKS. — The specimen from St. 281 is in bad condition, but the shape of the setae and the black pigment together with the number of segments and the prostomium agree with Pettibone's description and figures. However, the specimen from St. 194 lacked setae on segment 1.

DISTRIBUTION. — Antarctic (South Sandwich Isl.), Indian Ocean (E of South Africa and S of Ceylon). 2,553–4,360 m.

### *Paradiopatra paucibranchis* (Ehlers, 1908)

(Ehlers, 1908, pl. 10 figs 12–16, pl. 11 figs 1–6), Fig. 1.

RECORDS. — *Diopatra paucibranchis* Ehlers, 1908, p. 81. *Sarsonuphis paucibranchis* FAUCHALD, 1982, p. 77. *Paradiopatra paucibranchis* PAXTON, 1986, p. 38.

MATERIAL. — St. 182, SE of Durban, 33°28'S, 38°32'E, 5,110 m, SOT, one specimen: 18 x 1 mm (bad condition). St. 192, off Durban, 32°00'S, 32°41'E, 3,430 m, ST100, one specimen: 26 x 1 mm (anterior end). St. 550, NE of Sydney, 31°27'S, 153°33'E, 4,530 m, ST200, two specimens:20 x 1, 10 x 1 mm (anterior ends), four fragments. St. 665, Kermadec Trench, 36°38'S, 178°21'E, 2,470 m, HOT, six specimens: 32, 32, 28, 20 x 3 mm, 18 x 1, 20 x 1 mm (anterior ends), fragments, tubes. ? St. 668, Kermadec Trench, 36°23'S, 177°41'E, 2,640 m, HOT, one specimen: 10 x 0.5 mm (anterior part), one fragment. All in bad condition.

REMARKS. — All specimens have six rings on the ceratophores, ventral cirri are cirriform in the first three setigers and digitate posterior lobes are present in the first seven setigers. The beginning of branchiae varies between setigers 16–20, subacicular hooks are present in some specimens from setiger 9 (as in the holotype), but in some others from setiger 10.

DISTRIBUTION. — Antarctic Ocean, 63°16'S 57°51'E, 4,636 m, off South Africa, 3,430–5,110 m, Tasman Sea, 4,530 m, Kermadec Trench, 2,470 m.

## ORIGIN OF THE ABYSSAL POLYCHAETES

The abyssal fauna is probably derived from the bathyal fauna, from which species that can live under the high pressure and at low temperatures have spread downwards. LEVENSTEIN (1984) pointed out, on the basis of her analyses of the distribution of the deep-sea polynoids (especially the Macellicephalinae), that these polychaetes must have had two distribution centers, i.e., the eastern Atlantic Ocean and the western Pacific, which are the margins of the ancient Tethys Sea. However, during Oligocene (30–20 MY B.C.) the temperatures in abyssal depths decreased from around 10 °C to about 2 °C. This was shown by EMILIANI & EDWARDS (1953), who examined the oxygen isotopes of benthic Foraminifera of probably Oligocene age (30 MY) from the eastern part of the Central Pacific. This temperature change must have been catastrophic for abyssal and hadal faunas since only the eurythermic species survived.

The present polychaete fauna of the abyssal and hadalzones must be relics of a preglacial abyssal and hadal fauna, but besides these old components there must have been a new and still ongoing invasion of species from the bathyal zone to the abyss and to the hadal zone. LEVENSTEIN (1984) suggested that additional centers of distribution could be the eastern Pacific, the Arctic and the Antarctic.

The invasion to the hadal zone must have been from the abyss. LEVENSTEIN (1991) showed that of 80 identified species of polychaetes from this zone, 26 (32.5 %) were endemic to the trenches. Seventeen of these species were found to be endemic to only one trench, whereas the remaining nine were known from two-six

Source : MNHN, Paris

different trenches, some of them from neighbouring trenches, but also from trenches isolated by great distances in the Pacific Ocean. *Bathykermadeca hadalis* (KIRKEGAARD, 1956) (Polynoidae) is recorded from the Japan, Philippine, Yap, Kermadec, Bougainville and Banda trenches. This species is possibly a relict of an old preglacial polychaete fauna.

## DISCUSSION

As appears from this investigation, there is very little variation in morphology and size over large geographical distances. *Laetmonice benthaliana*, which is represented by a fairly large collection, showed no difference from East Africa to New Zealand and the Gulf of Panama and agreed with descriptions from the Antarctic and Central Pacific. Other species, i.e., *Leanira quatrefagesi*, *Bathyeliasona kirkegaardi* and *Bathyeliasona nigra* are represented in the material by fewer specimens, but all three species have been revised by PETTIBONE (1970, 1976) and no differences were found between specimens from localities separated by long distances, i.e., South America–Africa (*L. quatrefagesi*), Kermadec Trench, Aleutian Trench, and Portugal (*B. kirkegaardi*). PETTIBONE (1976) examined a small collection of *B. nigra* from the Antarctic, but her description and figures agree well with the present material from off South Africa and south of Ceylon. Similar to this, *Paradiopatra paucibranchis* was revised by FAUCHALD (1982) on a small collection from Antarctic. His redescription of the holotype agrees well with the "Galathea" material from south of Africa and east of Australia. A few characters varied from the holotype, i.e., the place where branchiae (setigers 17–36 compared to 16–20) and subacicular hooks begin (9 compared to 10), but this is also known for other species of the genus. *Aglaophamus elamellata* (Eliason, 1951) is a species which has only been recorded by me since the original description. However, I have a fairly large collection from Africa, Ceylon and Australia-New Zealand and compared them with the type and found no morphological differences.

Some of the material from the "Galathea" was badly damaged, but in many cases the setae of these damaged specimens were so characteristic that identification was possible. Many different sampling devices were used, but there were no connection between the number, the size or the condition of the specimens with the type of gear used. However, all material of the "Galathea" was washed through a 1.0 mm sieve. As mentioned before, many small polychaetes must have passed through these sieves. Later, I (1980) showed that when a 0.5 mm sieve is used, small polychaetes are retained on the screen. These species have a wide geographical distribution. Thus 78 % of the 23 species found in the northeastern abyssal part of the Atlantic, were common to the polychaetes in the abyssal area between New England and Bermuda.

## CONCLUSIONS

The present investigation shows that of the six named species from the "Galathea" expedition, four are distributed throughout the World, viz. *Leanira quatrefagesi*, *Aglaophamus elamellata*, *Bathyeliasona kirkegaardi* and *B. nigra*. The remaining two species: *Laetmonice benthaliana* and *Paradiopatra paucibranchis*, are recorded from the Indian Ocean and the Pacific and will probably be found in the Atlantic with additional studies.

Several abyssal species are shown to have a cosmopolitan distribution and several more probably occur. However, endemism in the deep sea does exist as was shown by LEVENSTEIN (1991) in her paper on the polychaetes in deep-sea trenches, in which 16 of the 26 hadal species in the trenches were endemic to one trench.

## REFERENCES

BRUUN, A.F., 1956. — The Abyssal Fauna: its ecology, distribution and origin. *Nature*, **177** : 1105–1108.

DAY, J.H., 1963. — The Polychaete Fauna of South Africa. Part 7: Species from Depths between 1,000 and 3,300 Metres West of Cape Town. *Ann. S. Afr. Mus.*, **46** : 353–371.

DAY, J.H., 1967. — *A Monograph of the Polychaeta of Southern Africa*. Brit. Mus. (Nat. Hist.), London, 878 pp.

EHLERS, E., 1908. — Die bodensässigen Anneliden aus Sammlungen der deutschen Tiefsee-Exped. *Wiss. Ergebn. deutsch. Tiefsee-Exped. Valdivia 1898–1899*, **16** : 1–168.

ELIASON, A., 1951. — Polychaeta. *Rep. Swed. Deep-Sea Exped.*, **2** : 129–148.

EMILIANI, C. & EDWARDS, G., 1953. — Tertiary Ocean Bottom Temperatures. *Nature*, **171**: 887–888.

Source : MNHN, Paris

FAUCHALD, K., 1982. — Revision of *Onuphis*, *Nothria* and *Paradiopatra* (Polychaeta: Onuphidae) Based upon Type Material. *Smithson. Contr. Zool.*, **356** : 1–109.

HARTMAN, O., 1964. — Polychaeta Errantia of Antarctica. *Antarctic Res. Ser. Washington*, **3** : 1–131.

HARTMAN, O., 1967. — Polychaetous Annelids Collected by USNS "Eltanin" and "Staten Island" Cruises Chiefly from Antarctic Seas. *Allan Hancock Monogr. mar. Biol.*, **2** : 1–387.

HARTMANN-SCHRÖDER, G., 1975. — Polychaeten der Iberischen Tiefsee gesammelt auf der 3. Reise der Meteor im Jahre 1966. *Mitt. Hamb. Zool. Mus. Inst.*, **72** : 47–73.

KIRKEGAARD, J.B., 1956. — Benthic Polychaeta from Depths Exceeding 6,000 Metres. – *Galathea Rep.*, **2** : 63–78.

KIRKEGAARD, J.B., 1980. — Abyssal Benthic Polychaetes from the Northeast Atlantic Ocean, Southwest of the British Isles. *Steenstrupia*, **6** : 81–98.

LEVENSTEIN, R.Y., 1962. — Polychaete Worms from Three Abyssal Trenches of the Pacific Ocean. *Zool. Zhur. Akad. Nauk SSSR*, **41** : 1142–1148.

LEVENSTEIN, R.Y., 1971. — Polychaete Worms of the Genus *Macellicephala* and *Macellicephaloides* (Family Aphroditidae) from the Pacific Ocean. *Trudy Inst. Okeanol. P.P. Shirshov Akad. Nauk SSSR*, **92** : 18–35.

LEVENSTEIN, R.Y., 1975. — The Polychaetous Annelids of the Deep-Sea Trenches of the Atlantic Sector of the Antarctic Ocean. *Trudy Inst. Okeanol. P.P. Shirshov Akad. Nauk SSSR*, **103** : 119–142.

LEVENSTEIN, R.Y., 1978a. — Polychaetes of the Family Polynoidae (Polychaeta) from the Deep-Water Trenches of the Western Part of the Pacific. *Trudy Inst. Okeanol. P.P. Shirshov Akad. Nauk SSSR*, **112** : 162–173.

LEVENSTEIN, R.Y., 1978b. — Annelida (Polychaeta) from the Deep Waters of the Pacific Region of Antarctic. *Trudy Inst. Okeanol. P.P. Shirshov Akad. Nauk SSSR*, **113** : 73–87.

LEVENSTEIN, R.Y., 1984. — On the Ways of Formation of the Deep-Sea Polychaeta Fauna of the Family Polynoidae. *In*: P.A. HUTCHINGS (ed), Proceedings of the First International Polychaeta Conference, Sydney. *Linn. Soc. New South Wales* : 72–85.

LEVENSTEIN, R.Y., 1991. — Distribution Patterns of Polychaeta in Deep-Sea Trenches. *Ophelia*, Suppl. **5** : 587–592.

MCINTOSH, W.C., 1885. — Report on the Annelida Polychaeta Collected by H.M.S. Challenger During the Years 1873–76. *Rep. Scient. Results explor. Voyage Challenger*, (Zool.), **12** : 1–554.

PAXTON, H., 1986. — Generic Revision and Relationships of the Family Onuphidae (Annelida: Polychaeta). *Rec. Aust. Mus.*, **38** : 1–74.

PETTIBONE, M.H., 1970. Revision of Some Species Referred to *Leanira* Kinberg (Polychaeta: Sigalionidae). *Smithson. Contr. Zool.*, No. **53** : 1–25.

PETTIBONE, M.H., 1976. — Revision of the Genus *Macellicephala* McIntosh and the Subfamily Macellicephalinae Hartmann-Schröder (Polychaeta: Polynoidae). *Smithson. Contr. Zool.*, **229** : 1–71.

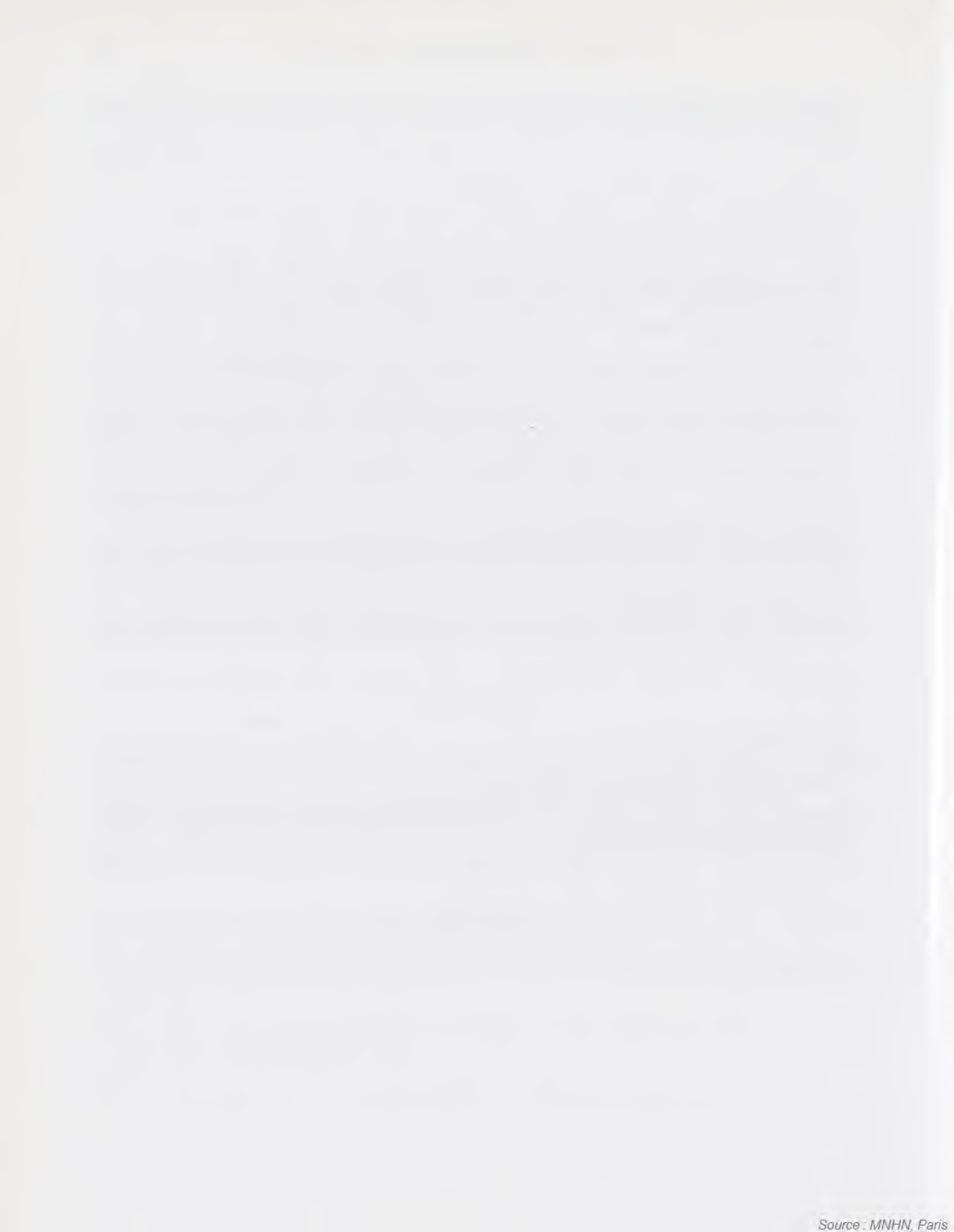
USCHAKOV, P.V., 1955. — Polychaete Worms of the Family Aphroditidae from the Kurile-Kamchatka Trench. *Trudy Inst. Okeanol. P.P. Shirshov Akad. Nauk SSSR*, **12** : 311–312. (In Russian, translated 1969 by the Israel Program for Scientific Transl. for the Bureau of Commercial Fisheries).

USCHAKOV, P.V., 1962. — Polychaetous Annelids of the Families Phyllodocidae and Aphroditidae from the Antarctic and Subantarctic. *Biol. Res. Soviet Antarct. Exped. 1955–58*, **1**: 129–189.

USCHAKOV, P.V., 1971. — On a New Abyssal Species of *Macellicephala* McIntosh (Polychaeta, Errantia) from the Aleutian Trench. Fauna of the Kurile-Kamchatka Trench. *Trudy Inst. Okeanol. P.P. Shirshov Akad. Nauk SSSR*, **96** : 36–40.

WESENBERG-LUND, E., 1962. — Reports of the Lund University Chile Expedition 1948–49. 43, Polychaeta Errantia. *Lunds Univ. Årsskr., N.F. Avd. 2*, **57** : 1–199.

Source : MNHN, Paris



Source : MNHN, Paris

# Preliminary results on recolonization in a small brackish basin on the island of Elba (western Mediterranean)

*Claudio LARDICCI & R. BALDI*

Dipartimento di Scienze dell'Ambiente e del Territorio
V. Volta 6, 56126 Pisa, Italy

ABSTRACT

The recolonization of polychaetes in a small brackish basin of Elba Island has been studied to determine how the abundant species respond to artificial disturbance. Results have shown that recolonization in this small brackish basin was characterized by two species (*Capitella* cf. *capitata* and *Brania oculata*), that colonized the substrate in every months.

RÉSUMÉ

**Résultats préliminaires sur la recolonisation d'un petit bassin saumâtre de l'île d'Elbe (Méditerranée occidentale)**

La recolonisation d'un peuplement de Polychètes d'un petit bassin saumâtre de l'île d'Elbe a été étudiée pour mettre en évidence les réponses des espèces les plus abondantes à une défaunation artificielle. Les résultats ont mis en évidence que la recolonisation est caractérisée par *C.* cf. *capitata* et *B. oculata*. Ces espèces sont capables de coloniser le substrat défauné pendant tous les mois étudiés et d'être dominantes au cours des premières phases de la succession.

## INTRODUCTION

The recolonization of polychaete assemblage (we defined as assemblage the ensemble of the most abundant species which characterized the community) in a small brackish basin of Elba Island was the purpose of this study. This assemblage has shown high persistence in time, due to the characteristics adaptive strategies of its species (LARDICCI, 1991). The successional sequences in zoobenthos have been studied extensively in recent years through the use of experimental boxes (GUÉRIN, 1970; MASSÉ & GUÉRIN, 1978; MCCALL 1978; ARNTZ & RUMOHR, 1982; ZAJAC & WHITLATCH, 1982a, b; LEVIN, 1984; WHITLATCH & ZAJAC, 1985; DIAZ-CASTANEDA, 1987; DIAZ-CASTANEDA & SAFRAN, 1988; DIAZ-CASTANEDA *et al.*, 1989; FRID, 1989; BERGE, 1990). However, concerning the successional dynamics and the response of polychaete assemblage along the Mediterranean coasts to artificial disturbances, few data exist (DIAZ-CASTANEDA & SAFRAN, 1988; LARDICCI 1992).

LARDICCI, C. & R. BALDI, 1994. — Preliminary results on recolonization in a small brackish basin on the island of Elba (western mediterranean). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 479-483. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## MATERIAL AND METHODS

The studied area (called Salina) is located in Portoferraio Bay, Elba Island (Fig. 1). It is a shallow intertidal basin, surrounded by a series of barriers which permit water exchange only during high tide. A small drainage channel is a major input of fresh water into the basin. The dynamics and the general feature of recruitment in this basin have been previously described (LARDICCI, 1991, 1992).

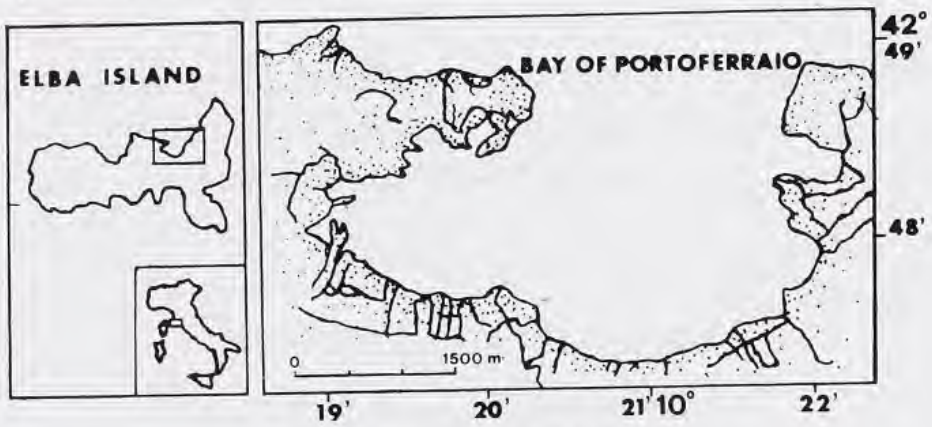



FIG.1. — Study area and sampling station.

Recolonization was studied by deploying experimental boxes (50 x 50 x 20 cm) containing defaunated air dried sediment in a silty-sand area which measures 5 x 5 m. All boxes were dug into sediment with the top of the box flush with the surface of the sediment.

Two series of experiments were performed: the first consisted of boxes that were sampled, removed and replaced monthly to determine monthly settlement from July 1990 to November 1991. These boxes were referred to as the monthly boxes. The second experiment consisted of seven boxes which were deployed at the start of the study on July 9, 1990 and sampled after 7, 14, 30, 60, 120, 240 and 477 days to follow recolonization. These boxes were referred to as the successional boxes.

Samples were collected using corers with a 6 cm inside diameter and pushed 20 cm into the sediment during low tide. Four cores per month were taken from the monthly boxes, four from the successional boxes for each sampling date and four from the natural sediment. We wish to emphasize that the observations concerning the experimental boxes and natural sediment are to be considered as comparisons of physical locations, rather than treatment *per se* (HURLBERT, 1984) and a great deal of caution must be employed in the interpretation of the results. Samples were washed through a 250 µm sieve. Sample residues were fixed in 4 % formalin. All samples were sorted under a dissecting microscope and all animals, where it was possible, identified to species. Polychaetes were the most important group collected (68.7 %) while molluscs and crustacean constituted respectively the 25 % and 6.3 % of the total species. Twenty-two species of polychaetes belonging to 10 families were collected during the course of this study (Table 1).

The temperature in the water ranged from 11.9 °C in January 1991 to a high value of 35.4 °C in July 1991. Salinity ranged from 30.6 P.S.U. in May 1991 to 38.3 P.S.U. in September 1991 in the study period.

## RESULTS

Monthly sampled boxes: polychaetes were the only species of macrozoobenthos with many unidentified turbellarians and nematods collected in experimental boxes. These species were *Capitella* cf. *capitata*, *Brania oculata*, *Streblospio shrubsolii*, *Perinereis rullieri*, *Syllides edentata* and *Cirrophorus furcatus*. *Capitella* cf. *capitata* was the most abundant species collected from the boxes with a pattern that seemed to follow its fluctuations in the ambient. *B. oculata* and *S. shrubsolii* were present nearly every month but their distribution in the boxes was quite different from that of their ambient numerical levels. *S. shrubsolii* showed large fluctuations in the natural sediment, whereas, there were fewer specimens within the box. *B. oculata* was abundant in the ambient but showed a low level of abundance nearly all the months. *P. rullieri* appeared to colonize the

Source : MNHN, Paris

defaunated sediment only from March through July 1991, *S. edentata* was present in the last four months of 1990, and June and July 1991, *C. furcatus* was only collected in September 1990.

Successional trends: polychaetes were the only species of macrozoobenthos with many unidentified turbellarians and nematods collected up to 120 days in these boxes. The amphipod *Melita palmata* and the tanaidacean *Leptochelia savigny* were also present after 120 days with few specimens while the bivalve *Abra ovata* began to appear at 477 days in this box. Only *C.* cf. *capitata* and *B. oculata* were collected at the first phase of succession. *C.* cf. *capitata* showed a relatively constant numerical increase from 30 to 240 days after which it declined. Fewer *B. oculata* occurred for the first 60 days then it continued to increase until 240 days after which the number of specimens remained at the same level to the end of the experiment. Three additional species appeared at 120 days; these were *S. shrubsolii* which reached its highest level at 477 days, *M. fuliginosus* decreased after its appearance and continued to decline in number to the end of the experiment and *S. edentata* fluctuated in its occurrence during the remainder of the experiment. *P. rullieri* was only present at 240 days, *D. ornata* appeared at 240 days and decreased and *C. furcatus* colonized the defaunated sediment at 477 days (Fig. 2).

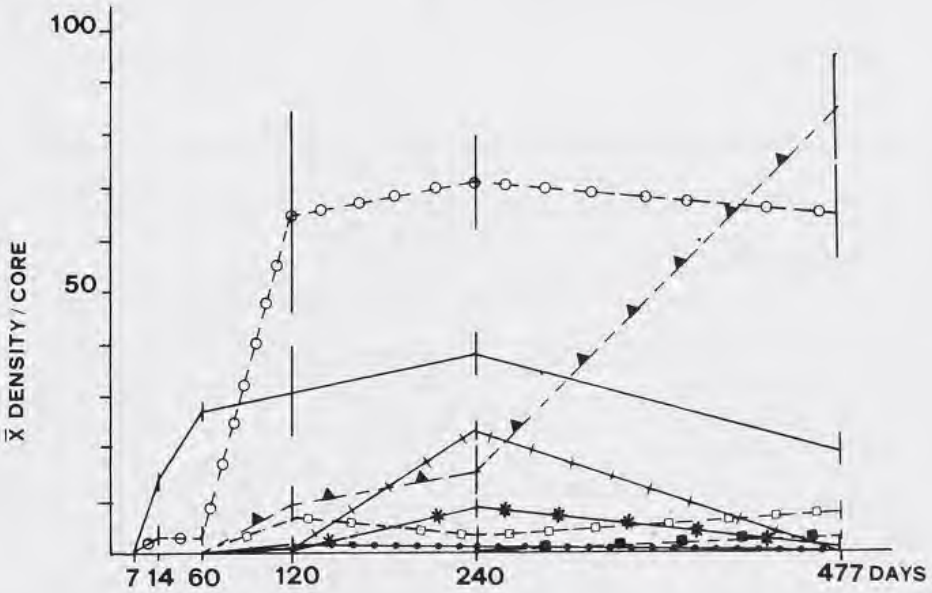



FIG. 2. — Successional trends of the collected species in the experimental boxes. The error bars are standard errors.

*C. cf. capitata* ——— *B. oculata* o—o—o—o;
*S. shrubsolii* ▲—▲—▲—▲ *S. edentata* □—□—□—□;
*M. fuliginosus* •——•——•——• *P. rullieri* +——+——+——+;
*C. tentaculata* ■—■—■—■ *D. ornata* ✱—✱—✱—✱;

## DISCUSSION

Life-history features are important factors that allow settling and exploitation of the disturbed habitats (ZAJAC & WHITLATCH, 1982a , b; WHITLATCH & ZAJAC, 1985; DIAZ-CASTANEDA & SAFRAN, 1988). Most of the species collected in monthly boxes are considered opportunistic but only *B. oculata* and *C.* cf. *capitata* were able to colonize the defaunated habitat in all the study months. The settling periods of many species which were present within experimental boxes were observed between May and September (LARDICCI, 1992). Recolonization could also be due to both postlarvae and adult movements in addition to larval settlement. The presence of benthic adults in the water column was previously reported in this basin (LARDICCI, 1992) and it may be of importance in maintaining the persistence of the assemblage in shallow water (LEVIN, 1984; FRID, 1989). Variability in recolonization may be explained by fluctuations in abiotic parameter fluctuations. Many of the species were

Source : MNHN, Paris

surface or near surface deposit-feeders, and their food resource could be influenced by processes such as sedimentation, resuspension and transport of particulate organic matter (ZAJAC & WHITLATCH, 1982a). Fifteen days after the setting of experimental boxes, the substrate was covered by a thin layer of sediment which had been resuspended and deposited by the tidal current. This sediment constituted a very favourable habitat for *B. oculata* and *C.* cf. *capitata*; this last species was particularly attracted by organically enriched sediment (DIAZ-CASTANEDA *et al.*, 1989; TSUTSUMI, 1990; TSUTSUMI et al., 1990). The time of disturbance was another important factor which could affect the processes of settlement (ZAJAC & WHITLATCH, 1982b; DIAZ-CASTANEDA *et al.*, 1989). In the period beginning in July an early phase was noted up to 60 days in which only *C. cf. capitata* and *B. oculata*. This was followed after 120 days with the occurrence of other species such as *S. shrubsolii*, *S. edentata* and *M. fuliginosus* began to appear. *C.* cf. *capitata* is a well-known opportunistic species (GRASSLE & GRASSLE, 1974) and it appeared able to colonize successfully the defaunated sediment both in successional and monthly experiment in this basin. *B. oculata* is not a so-called opportunistic species but the presence of external gestation and adult mobility could be the mechanisms that allow this species to quickly colonize the substrate. Colonization by postlarval stages, and particularly by adults carrying a full complement of young, permits extremely rapid local increases in population size following very few colonization events (LEVIN, 1984). Hence the recolonization in this small brackish basin was characterized by two species (*B. oculata* and *C.* cf. *capitata*) which are able to colonize the substrate in all months of the study and were the dominant species in the initial phase of successional dynamics. Future research will have to clarify if the observed trend was only a matter of seasonal effect or a constant rule in this basin.

TABLE 1. — List of species.

| | |
|---|---|
| PARAONIDAE | *Pionosyllis* sp. |
| *Cirrophorus furcatus* Hartman, 1957 | *Brania oculata* Hartman-Schröder, 1960 |
| SPIONIDAE | *Exogone naidina* Oersted, 1845 |
| *Malacoceros fuliginosus* (Claparède, 1870) | NEREIDAE |
| *Spio decoratus* Bobretzky, 1870 | *Nereis diversicolor* Müller O. F., 1776 |
| *Spiophanes bombyx* (Claparède, 1870) | *Perinereis rullieri* Pilato, 1974 |
| *Streblospio shrubsolii* (Buchanan, 1890) | *Perinereis cultrifera* (Grube, 1840) |
| *Prionospio malmgreni* Claparède, 1870 | ONUPHIDAE |
| CIRRATULIDAE | *Hyalinoecia* sp. |
| *Cirriformia tentaculata* (Montagu, 1808) | DORVILLEIDAE |
| CAPITELLIDAE | *Pettiboneia urciensis* Campoy & San Martin, 1980 |
| *Capitella* cf. *capitata* (Fabricius, 1780) | *Protodorvillea kefersteinii* (Mc Intosh, 1865) |
| *Heteromastus filiformis* (Claparède 1864) | SABELLIDAE |
| SYLLIDAE | *Desdemona ornata* Banse 1957 |
| *Syllides edentata* Westheide, 1974 | LUMBRINEREIDAE |

## ACKNOWLEDGEMENTS

We would like to thank Prof. D. J. REISH for the critical revision of the manuscript and two anonymous rewiers for comments and suggestions.

## REFERENCES

ARNTZ, W. E. & RUMOHR H., 1982. — An experimental of macrobenthic colonization and succession and the importance of seasonal variation in temperature latitudes. *J. Exp. Mar. Biol. Ecol.*, **64** : 17-45.

BERGE, J. A., 1990. — Macrofauna recolonization of subtidal sediments. Experimental studies on defaunated sediment contamined with crude oil in two Norwegian fjords with unequal eutrophication status. I. Community responses. *Mar. Ecol. Prog. Ser.*, **66**: 103-115.

DIAZ-CASTANEDA, V., 1987. — Recolonisation benthique d'un sédiment dans des enceintes expérimentales replacées dans le milieu naturel (étage infralittoral d'une baie méditerranéenne, Toulon, France). *Cah. Biol. mar.*, **28** : 551-566.

DIAZ-CASTANEDA, V. & SAFRAN, P., 1988. — Dynamique de la colonisation par les annélides polychètes de sédiments défaunés par la pollution dans des enceintes expérimentales en rade de Toulon (France). *Ocean. Acta*, **3** : 285-297.

Source : MNHN, Paris

DIAZ-CASTANEDA, V., RICHARD, A. & FRONTIER, S., 1989. — Preliminary results on colonization, recovery and succession in a polluted area of southern North Sea (Dunkerque's harbour, France). *Scient. Mar.*, **53** : 705-716.

FRID, C. L. J., 1989. — The role of recolonization processes in benthic communities, with special reference to the interpretation of predator-induced effects. *J. exp. mar. Biol. Ecol.*, **126** : 163-171.

GRASSLE, J. F. & GRASSLE, J. P., 1974. — Opportunistic life histories and genetic systems in marine benthic Polychaetes. *J. mar. Res.*, **32** : 253-284.

GUERIN, J. P., 1970. — Étude expérimentale de l'établissement d'un peuplement de substrat meuble à partir de larves méroplanctoniques. *Cah. Biol. mar.*, **11** : 167-185.

HURLBERT, S. H., 1984. — Pseudoreplication and the design of ecological field experiments. *Ecol. Mon.*, **54** : 187-211.

LAMBSHEAD, P. J., PLATT, H. M. & SHAW, K. M., 1983. — The detection of differences among assemblages of marine benthic species based on assessment of dominance and diversity. *J Nat. Hist.*, **17** : 859-874.

LARDICCI, C., 1991. — Le peuplement de polychètes d'un petit bassin saumâtre de l'île d'Elbe (Mer Méditerrannée). *Vie Milieu*, **41** : 195-201.

LARDICCI, C., 1992. — General characteristics of recruitment and recolonization in Polychaete assemblage in a small brackish basin on the island of Elba (Western Mediterranean). *Oebalia*, **18** : 69-81.

LEVIN, L., 1984. — Life history and dispersal patterns in a dense infaunal Polychaetes assemblages: community structure and response to disturbance. *Ecology*, **65** : 1185-1200.

MASSÉ, H. & GUÉRIN, J. P, 1978. — Etude expérimentale sur le recrutement des espèces de la macrofaune benthique des substrat meubles. Données sur les cycles biologiques des Polychètes et des Bivalves. *Tethys*, **8** : 283-294.

MCCALL, P.,1978. — Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *Journ mar. Res.*, **35** : 221-266.

TSUTSUMI, H., 1990. — Population persistence of *Capitella* sp. (Polychaeta; Capitellidae) on a mud flat subject to environmental disturbance by organic enrichment. *Mar. Ecol. Prog. Ser.*, **63** : 147-156.

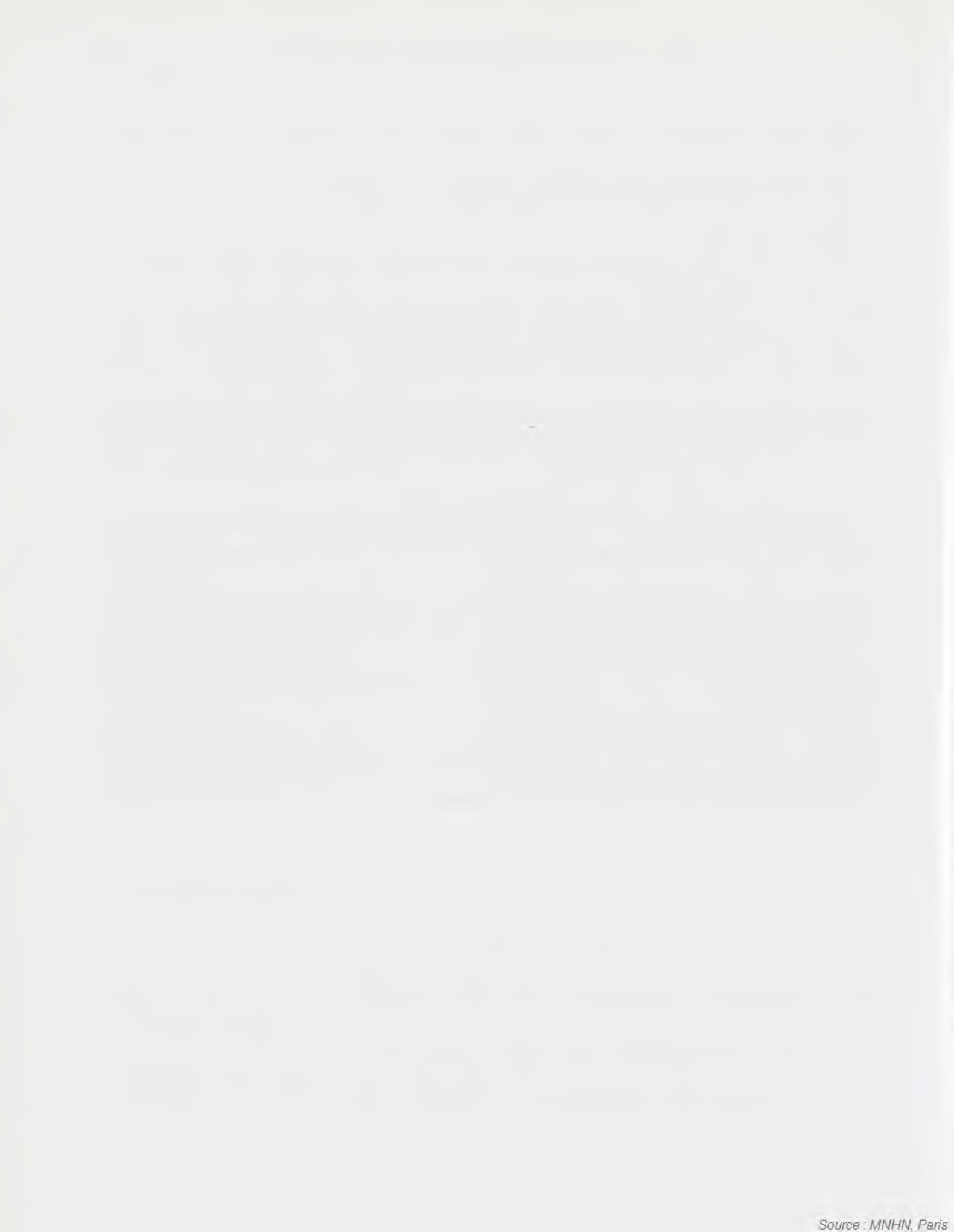
TSUTSUMI, H., FUKUNAGA, S., FUJITA, N. & SUMIDA, M., 1990. — Relationship between growth of *Capitella* sp. and organic enrichment of the sediment. *Mar. Ecol. Prog. Ser.*, **63** : 157-162.

WHITLATCH, R. B. & ZAJAC, R. N., 1985. — Biotic interactions among estuarine infaunal opportunistic species. *Mar. Ecol Prog. Ser.*, **21**: 299-311.

ZAJAC, R. N. & WHITLATCH, R. B., 1982a. — Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Mar. Ecol. Progr. Ser.*, **10** : 1-14.

ZAJAC, R. N. & WHITLATCH, R. B., 1982b. — Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Mar. Ecol. Prog. Ser.*, **10** : 15-27.

Source : MNHN, Paris



Source : MNHN, Paris

# Intertidal sandy beaches Polychaetes of São Sebastião island, southern Brazil

*Eloisa H. MORGADO*, A. Cecilia Z. AMARAL**
*Edmundo F. NONATO** & Lara B. SALVADOR****

* Depto. Zoologia, IB - UNICAMP. CP:6109
13081-970 - Campinas, SP, Brazil
** Depto. Oceanografia, Biologia, IO - USP. CP: 9075
05508 - São Paulo, SP, Brazil
*** Pós-Graduação, UNESP
Rio Claro, SP, Brazil

## ABSTRACT

The composition and distribution of polychaete fauna along sandy beaches of São Sebastião Island (southern Brazil) and their relation with sediment variables were examined. Functional feeding groups were used to investigate distribution patterns of intertidal polychaetes. The beaches were dominated by detritivores. Surface-deposit feeders and suspension-feeders presented higher relative abundances in very fine sand, whereas carnivorous polychaetes and subsurface-deposit feeders were more abundant in coarser sands. The proportion of subsurface-deposit feeders increased in medium sediments with higher percentages of organic carbon. Sessile polychaetes generally inhabited physically stable habitats, and occurred in low proportion. The distribution and abundance of feeding groups seem to be related to sedimentary conditions and environmental stability.

## RÉSUMÉ

**Polychètes intertidaux des plages sableuses de l'île de São Sebastião, Brésil méridional**

La composition et la distribution de la faune de polychètes ont été examinées de long des plages sablonneuses de l'Ile de São Sebastião (Brésil méridional) en relation avec les caractéristiques sédimentaires. Les modèles de distribution des polychètes intertidaux ont été recherchés en utilisant les groupements fonctionnels alimentaires. La distribution et l'abondance selon les groupes trophiques paraissent en relation avec les conditions sédimentaires et la stabilité du milieu. Il a été observé que 1) les espèces détritivores sont numériquement dominantes dans les groupements macrobenthiques, la classe trophique des détritivores de surface étant la plus abondante ; 2) la proportion de ces derniers et des suspensivores peu mobiles atteint son maximum dans le sable très fin, tandis que les espèces carnivores ont leur plus grande abondance dans les sables grossiers ; 3) les détritivores de subsurface sont dominants dans la plupart des habitats et leur abondance croît dans les sédiments moyens avec les taux le plus élevés de carbone organique ; 4) les espèces sessiles se rencontrent généralement dans les habitats physiquement stables.

---

MORGADO, E.H., AMARAL, A.C.Z., NONATO, E.F. & L.B. SALVADOR, 1994. — Intertidal sandy beaches Polychaetes of São Sebastião island, southern Brazil *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 485-492. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

Sediment structure is an important factor determining organization of soft-bottom benthic communities. The inter-relationships of habitat, resource availability, and feeding mechanisms are fundamental aspects of the animal-sediment interactions. In this regard, trophic group analysis can play a significant role in the determination of distribution patterns and benthic community organization (SANDERS, 1958; LEVINTON, 1972; WHITLATCH, 1980, 1981).

Polychaetes have a relevant participation in the productivity of marine ecosystems. They present high levels of trophic functional diversity (FAUCHALD & JUMARS, 1979) allowing their application on the determination of soft-bottom communities trophic structure (MAURER & LEATHEM, 1981; BIANCHI & MORRI, 1985; PAIVA, 1990). However, information on polychaete feeding biology and trophic-group interactions is limited for the intertidal system.

The purpose of this study was to define the polychaete fauna composition and to examine aspects such as feeding biology and trophic structure of the macrobenthic species along beaches of São Sebastião Island. Sediment attributes of the intertidal region, i.e., granulometry and organic-matter content were also studied and used to interpret the spatial patterns of polychaete trophic-groups. Species distribution patterns and polychaete community structure of these beaches were described by AMARAL *et al.* (in press).

## MATERIAL AND METHODS

The polychaete fauna of 12 beaches on the innerside of São Sebastião Island, southeastern Brazilian coast (23°44' to 23°52'S - 45°21' to 45°26'W), was examined between May 1990 and March 1991. The island is separated from the mainland by a deep channel (Fig. 1). Many contiguous protected beaches are present on the north side. The intertidal zone is usually relatively narrow, but may increase in size because of sand or boulder barriers covered with the angiosperm *Halodule*. The central part of the island is a typical low energy environment with a wide intertidal zone and gently sloping gradients. Small narrow beaches with steep slopes characterize the exposed southern coast.

Eighty two biological samples were taken from the intertidal region. The macrofauna was collected from within a rectangular iron sampler of 0.025 $m^2$ and 10 cm depth. Two replicates were taken at each station. The sediment was washed through sieves of 1.0 and 0.5 mm mesh. The organisms retained were preserved in 70 % alcohol for later identification. Parallel sediment samples were taken. These were dry sieved for granulometric analyses (SUGUIO, 1973). The organic matter content was determined by calcination (AMOUREUX, 1966).

All polychaetes present were classified according to trophic categories proposed by FAUCHALD & JUMARS (1979). Each species was allocated to one of these classes on the basis of their gut-contents and previous studies. Since beach sediments are continuously ressuspended by wave action, the detritivores were subdivided into surface, subsurface and suspension feeders. Some species were assigned to more than one trophic group because they have alternative feeding mechanisms.

## RESULTS

Polychaetes were absent from the samples taken from the southern and northern exposed beaches. A total of 1765 individuals in 38 species were present in the samples from seven beaches.

The beaches of Barra Velha, Perequê, Engenho d'Água, Fora and Siriuba had a largest number of species and specimens (Table 1). The greatest polychaete densities (ind. 0.05 $m^{-2}$) were *Scolelepis squamata* (304) at Siriuba ; *Heteromastus filiformis* (96), *Capitella capitata* (66), *Laeonereis acuta* (64), and *Isolda pulchella* (33) at Barra Velha ; *Scoloplos* (*Leodomas*) sp. (22), and *Owenia fusiformis* (16) at Fora, and *Armandia agilis* (15) at Perequê.

Detritivores numerically dominated the polychaete fauna, comprising 96 % of the individuals. Surface deposit-feeders, primarily represented by *S. squamata*, *C. capitata*, and *I. pulchella*, were the most abundant feeding group throughout the area (39.1 %) (Fig. 2). Subsurface deposit-feeders (36.2 %) dominated the central part of the island (Barra Velha) which had the highest concentration of organic matter (Table 1). *L. acuta*, *S.* (*Leodamas*) sp. and *H. filiformis* were the most abundant of the 10 species present. The proportion of suspension feeders was low in most beaches and increased at Siriuba and Garapocaia (Fig. 2) due to abundance of *S. squamata*. Carnivores were the less abundant feeding group (4.2 %) and were mainly represented by *Langerhansia cornuta*, *Marphysa sanguinea*

Source : MNHN, Paris

FIG. 1. — Location of the station locations at São Sebastião Island.

and *Lumbrinereis tetraura*. The number of carnivores was greatest in very coarse sand at Perequê, Engenho D'Água and Fora.

The most abundant and diverse polychaete fauna occurred in medium sands (Fig. 3). Mobile subsurface deposit-feeders and carnivores were dominant in coarse grains. On the other hand, surface deposit-feeders and suspension feeders were rare or absent in coarser grains and increased in numbers in fine sands.

Motile polychaetes were common in coarse and medium sediments, while discretely motile ones preferred very fine sand. Sessile polychaetes, although more abundant in medium grains, were present in low proportions (< 20 %) in all substrates.

Jawed forms were rare, whereas soft-proboscis species occurred in high proportions (> 30 %) in all sediments, except in very fine sand. Tentaculate species dominated in fine sands (96 %) as surface detritivores and suspension-feeders.

Source : MNHN, Paris

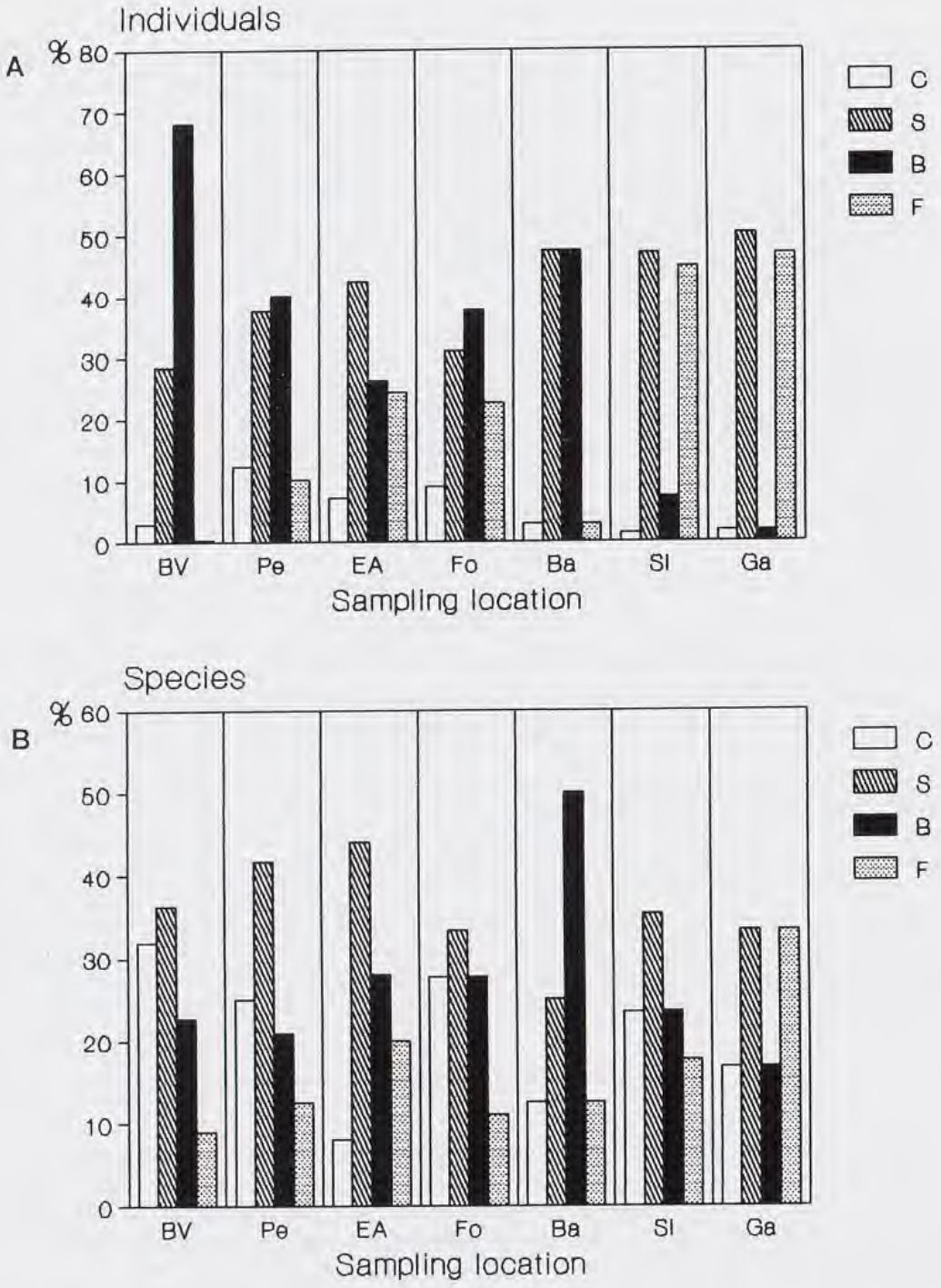



FIG. 2. — Trophic groups distribution (A= individuals and B= species, in percentage) at different sampling locations: Barra Velha (BV); Perequê (Pe); Engenho D'Água (EA); Fora (Fo); Barreiros (Ba); Siriúba (Si); Garapocaia (Ga). Carnivore (C); Surface deposit-feeders (S); Subsurface deposit-feeders (B); Suspension-feeders (F).

Source : MNHN, Paris

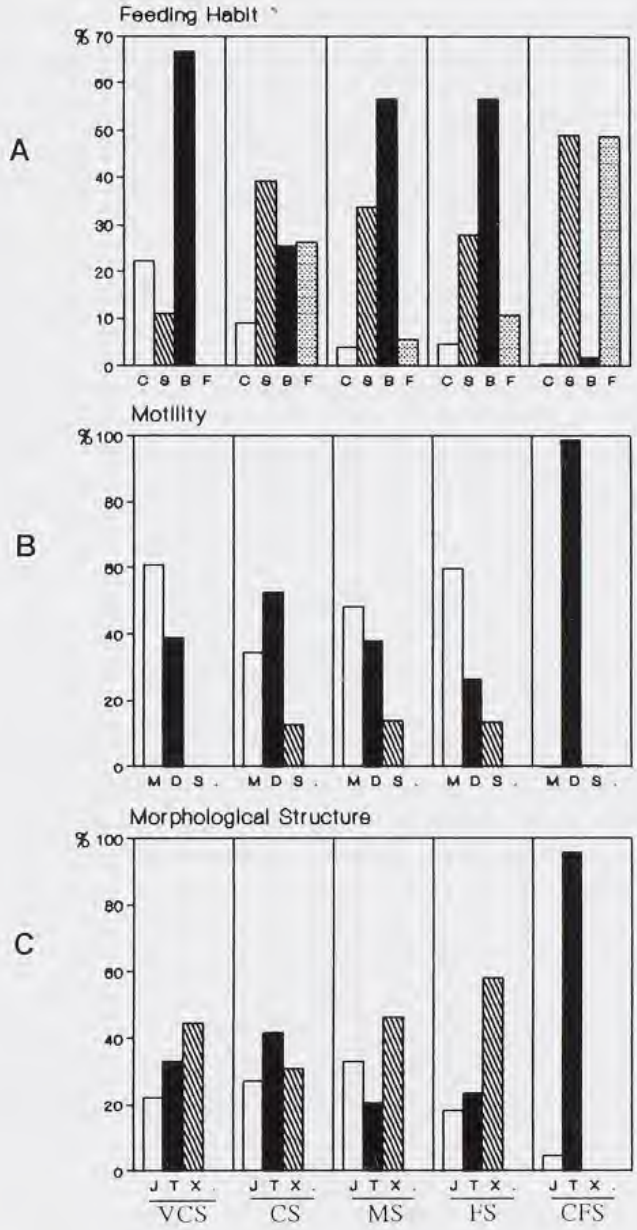



FIG. 3. — Individual percentages of feeding habitats (A), motility (B) and morphological structure (C), in granulometric classes. Categories: Carnivore (C); Surface deposit-feeders (S); Subsurface deposit-feeders (B); suspension-feeders (F); Motile (M); Discretely motile (D); Sessile (S); Jawed (J); Tentaculate (T); Other structures (X). (VCS: very coarse sand; CS: coarse sand; MS: medium sand; FS: fine sand; CFS: very fine sand).

Source : MNHN, Paris

TABLE 1. — Sediment average physico-chemical parameters, and polychaete species occurrence, total number of individuals and functional trophic groups (FTG), at different sampling site: Barra Velha (BV) ; Perequê (Pe) ; Engenho D'Água (EA) ; Fora (Fo) ; Barreiros (Ba) ; Siriúba (Si) ; Garapocaia (Ga).

| SAMPLING LOCATIONS | BV | Pe | EA | Fo | Ba | Si | Ga | | |
|---|---|---|---|---|---|---|---|---|---|
| SAMPLING NUMBERS | 17 | 14 | 08 | 07 | 02 | 08 | 06 | | |
| SAND (%) coarse | 18.10 | 19.22 | 13.62 | 30.38 | 12.07 | 11.64 | 17.65 | | |
| SAND (%) medium | 15.82 | 15.51 | 16.66 | 18.76 | 16.73 | 10.12 | 16.85 | | |
| SAND (%) fine | 19.27 | 16.06 | 34.98 | 10.27 | 39.10 | 30.68 | 29.23 | | |
| ORGANIC MATTER (%) | 4.71 | 2.64 | 1.33 | 0.61 | 0.70 | 3.30 | 2.30 | TOTAL | FTG |
| *Podarke pallida* (Claparède, 1864) | 1 | | | | | | | 1 | CMJ |
| *Loandalia americana* Hartman, 1947 | 1 | 1 | | 4 | | 2 | | 8 | CMJ |
| *Sigambra grubii* O.F. Müller, 1858 | 1 | | | | | 3 | 1 | 5 | CMJ |
| *Langerhansia cornuta* (Rathke, 1843) | | 7 | 5 | 1 | 1 | | | 14 | CMJ |
| *Ceratonereis mirabilis* Kinberg, 1866 | | 11 | 4 | | | | | 15 | BDJ |
| *Laeonereis acuta* (Webster, 1879) | 233 | | | 26 | | 32 | | 291 | BDJ |
| *Glycera americana* Leidy, 1855 | 1 | 1 | | | | | | 2 | CDJ |
| *Glycinde multidens* Müller, 1858 | 4 | | | 2 | | | | 6 | CDJ |
| *Goniada littorea* Hartman, 1950 | | 3 | | | | | | 3 | CDJ |
| *Diopatra cuprea* (Bosc, 1802) | 2 | 11 | | 4 | | | | 17 | SDJ |
| *Diopatra ornata* Moore, 1911 | | 26 | 7 | | | | | 33 | SDJ |
| *Diopatra splendidissima* Kinberg, 1865 | 3 | | | | | | | 3 | SDJ |
| *Marphysa sanguinea* Nonato, 1965 | 5 | 13 | | 7 | | 5 | | 30 | CDJ |
| *Nematonereis hebes* (Montagu, 1815) | | | 3 | | | | | 3 | CDJ |
| *Lumbrineris tetraura* (Schmarda, 1861) | 9 | 10 | | 1 | | 1 | | 21 | CMJ |
| *Haploscoloplos fragilis* (Verrill, 1873) | 1 | | | | | | | 1 | BMX |
| *Naineris setosa* (Verrill, 1900) | | | 5 | 1 | 3 | | | 9 | BMX |
| *Scoloplos (Leodamas)* sp. | 24 | 44 | 1 | 24 | 1 | 16 | | 110 | BMX |
| *Aricidea fragilis* Webster, 1879 | 1 | | | | | 1 | | 2 | SMX |
| *Dispio remanei* Friedrich, 1956 | 1 | | 1 | | | | | 2 | SDT/FDT |
| *Laonice branchiata* Nonato, 1981 | | | 1 | | | | | 1 | SDT/FDT |
| *Polydora websteri* Hartman, 1943 | | | | | | 2 | | 2 | SDT/FDT |
| *Prionospio dayi* (Foster, 1969) | | | | | | 6 | | 6 | SDT/FDT |
| *Prionospio steenstrupi* Malmgren, 1867 | | | 5 | | | | | 5 | SDT/FDT |
| *Scolelepis squamata* (Müller, 1806) | | 15 | | 12 | 1 | 362 | 28 | 41 | SDT/FST |
| *Magelona variolamellata* Bolivar e Lana, 1986 | | 3 | 4 | | | | | 7 | SDT |
| *Chaetopteras variopedatus* (Renier, 1804) | | 1 | 2 | | | | | 3 | SDT/FST |
| *Cirriformia tentaculata* (Montagu, 1808) | | 20 | 2 | | | | | 22 | SMT |
| *Armandia agilis* (Andrews, 1891) | 6 | 26 | 9 | 1 | 11 | 9 | | 62 | BMX |
| *Capitella capitata* (Fabricius, 1780) | 109 | 5 | 3 | 2 | 16 | 5 | 2 | 142 | SMX |
| *Heteromastus filiformis* (Claparède, 1864) | 261 | 33 | 4 | | | | 1 | 299 | BMX |
| *Mediomastus californiensis* Hartman, 1944 | | | | 10 | 2 | 4 | | 16 | BMX |
| *Nonatus longilineus* Amaral, 1980 | | 1 | 1 | | | | | 2 | BMX |
| *Notomastus lobatus* Hartman, 1947 | | | 5 | | | | | 5 | BMX |
| *Owenia fusiformis* delle Chiaje, 1841 | 2 | 13 | 18 | 25 | | | | 58 | SDT/FST |
| *Isolda pulchella* F. Müller, 1858 | 101 | 11 | 1 | 4 | | 13 | | 130 | SST |
| *Loimia medusa* (Savigny, 1818) | | 3 | 3 | 4 | | | | 10 | SST |
| *Terebellides anguicomus* (F. Müller, 1858) | 1 | | | | | | | 1 | SST |
| TOTAL OF INDIVIDUALS | **767** | **258** | **84** | **128** | **35** | **461** | **32** | **1765** | |
| SPECIES NUMBER/LOCATION | **20** | **21** | **20** | **16** | **7** | **14** | **4** | **38** | |

## DISCUSSION

Low-density polychaete assemblages characterized the area. In physically stressed environments, such as the intertidal sandy beaches, dense assemblages seldom, if ever, develop. In this situation recruitment and abiotic factors such as turbulence tend to maintain population densities at low-levels (WILSON, 1984). On the other hand, in physically stable habitats, population densities increase, so that competition and predation regulate community structure (PETERSON, 1979). Habitat differences in sediment structure related to local hydrological conditions determined the distribution of trophic groups and consequently the community structure. Similar observations were reported by GASTON & NASCI (1988), and GASTON *et al.* (1988) in estuaries in Louisiana.

Surface deposit-feeders dominated most beaches because they can explore a wider resource spectrum in the sediment/water interface (EAGLE & HARDIMAN, 1977; JOSEFSON, 1986). Species which are able to use alternative strategies, such as Oweniidae and Spionidae (either surface-deposit feeders or suspension feeders), are able to occupy rich organic sediments as well as sediments with large amounts of suspended material. *Scolelepis squamata*, the most abundant spionid, presents morphological and ethological adaptations which allow its survival in harsh environments. Unlike other spionids it has permanent palps, allowing the occupation of sand habitats

Source : MNHN, Paris

where deciduous palps are easily lost by the action of turbulence and where predation rates are low (DAUER, 1983).

Subsurface-deposit feeders are usually associated with very fine sediment particles and rich in organic matter (LANA, 1981; MAURER & LEATHEM, 1981; GASTON, 1987; MORGADO, 1988). Nevertheless, in this study these polychaetes were rare in very fine sand and dominated in other kind of sediments. At Barra Velha, for example, high levels of organic matter were found in medium and fine sand with large populations of *Laeonereis acuta* and *Heteromastus filiformis*. This beach is located in the island urban zone, with the sediments enriched by domestic sewage. According to DAUER & CONNER (1980), coarser sand sediments with low silt-clay contents and low nutrient retention capacity tend to be organically richer under moderate nutrient addition than finer sediments which is similar to this area.

Greater relative abundance of carnivorous polychaetes in coarser sediments is related to substrate physical characteristics. Many of the intertidal carnivores are small, depending on size of the sediment interstices to locomotion and prey capture (GASTON, 1987).

The dominance of motile forms and the scarcity of sessile ones reflect the dynamic sediment nature. In more stable habitats, with a high content of silt-clay and organic carbon, sessile polychaetes become more abundant (MAURER & LEATHEM, 1981; GASTON, 1987).

Detritivores distribution and abundance throughout the sites suggest that most of the particulate organic matter occurred in the sediment-water interface. In the richest sediments, resources were also available for subsurface deposit-feeders.

## ACKNOWLEDGEMENTS

This work is part of a project that studies the macrofauna of São Paulo state beaches, developed by the Zoology Department (IB - UNICAMP) with logistical support of the Marine Biology Center (CEBIMar - USP) and financial support of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundo de Apoio ao Ensino e Pesquisa (FAEP - UNICAMP). We are grateful to Elcio SOARES MARINHO (IB - UNICAMP) and ELSO (CEBIMar-USP technician) who were very helpful in field work and to Cláudia MAGALHÃES and Jacques VIELLIARD for assistance in manuscript preparation. Dr. Donald REISH and two anonymous reviewers improved very much earlier versions of the manuscript.

## REFERENCES

AMARAL, A.C.Z., MORGADO, E.H., PARDO, E.V. & REIS, M.O. (in press). — Estrutura da comunidade de poliquetos da zona entremarés em praias da Ilha de São Sebastião (SP). *Bolm. Inst. oceanogr.*, S. Paulo.

AMOUREUX, L., 1966. — Étude bionomique et écologique de quelques annélides polychètes de sables intertidaux des côtes ouest de la France. *Archs. Zool. exp. gén.*, **107** : 1-218.

BIANCHI, C.N. & MORRI, C., 1985. — I policheti come descrittori della strutura trofica degli ecosistemi marini. *Oebalia*, **11** : 203-214.

DAUER, D.M., 1983. — Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: Spionidae). *Mar. Biol.*, **77** : 279-285.

DAUER, D.M. & CONNER, W.G., 1980. — Effects of moderate sewage input on benthic polychaete populations. *Estuar. Coast. mar. Science*, **10** : 335-346.

EAGLE, R.A. & HARDIMAN, R.A., 1977. — Some observations on the relative abundance of species in a benthic community *In*: B.F. KEEGAN, P. O'CÉIDIGH & P.J.S. BOADEN (eds), *Biology of Benthic Organisms*. Pergamon Press, Oxford, New York : 197-208.

FAUCHALD, K. & JUMARS, P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. Ann. Rev.*, **17** : 193-284.

GASTON, G.R., 1987. — Benthic polychaeta of the Middle Atlantic Bight : feeding and distribution. *Mar. Ecol. Prog. Ser.*, **36** : 251-262.

GASTON, G.R. & NASCI, J.C., 1988. — Trophic structure of macrobenthic communities in the Calcasieu Estuary, Louisiana. *Estuaries*, **11** : 201-211.

Source : MNHN, Paris

GASTON, G.R., LEE, D.L. & NASCI, J.C., 1988. — Estuarine macrobenthos in Calcasieu Lake, Louisiana: community and trophic structure. *Estuaries*, **11**(3) : 192-200.

JOSEFSON, A.B., 1986. -- Temporal heterogeneneity in deep-water soft-sediment benthos - an attempt to reveal temporal structure. *Estuar. Coast. Shelf Science*, **23** : 147-169.

LANA, P.C., 1981. — *Padrões de Distribuição e Diversidade Específica de Anelídeos Poliquetos na Região de Ubatuba, Estado de São Paulo*. M. Sc. Thesis, Universidade de São Paulo, Instituto Oceanográfico, 111 pp.

LEVINTON, J.S., 1972. — Stability and trophic structure in deposit-feeding and suspension-feeding communities. *Amer. Natur.*, **106** : 472-486.

MAURER, D. & LEATHEM, W., 1981. — Polychaete feeding guilds from Georges Banks, USA. *Mar. Biol.*, **62** : 161-171.

MORGADO, E.H., 1988. — *Anelídeos Poliquetos do Sublitoral da Região de Ubatuba - SP, compreendida entre as Ilhas Anchieta e Vitória*. Ph. D. Thesis, Universidade Estadual de Campinas, Instituto de Biologia, 181 pp.

PAIVA, P.C., 1990. — *Padrões de Distribuição e Estrutura Trófica dos Anelídeos Poliquetos da Plataforma Continental do Litoral Norte do Estado de São Paulo*. M. Sc. Thesis, Universidade de São Paulo, Instituto Oceanográfico, 146 pp.

PETERSON, C.H., 1979. — Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. *In*: R.J. LIVINGSTON (ed), *Ecological Processes in Coastal and Marine Systems*. Plenum Press, New York : 233-264.

SANDERS, H.L., 1958. — Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.*, **3** : 245-258.

SUGUIO, K., 1973. — *Introdução a Sedimentologia*. Blucher/EDUSP, São Paulo, 312 pp.

WHITLATCH, R.B., 1980. — Patterns of resources utilization and coexistence in marine intertidal deposit-feeding communities. *J. mar. Res.*, **38** : 743-765.

WHITLATCH, R.B., 1981. — Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. *J. exp. mar. Biol. Ecol.*, **53** : 31-45.

WILSON, W.H., JR., 1984. — Non-overlapping distribution of spionid polychaetes: the relative importance of habitat and competition. *J. exp. mar. Biol. Ecol.*, **75** : 119-127.

Source : MNHN, Paris

# Influence of the tube-building spionid polychaete *Polydora ciliata* on benthic parameters, associated fauna and transport processes

*Carola Ilse-Marie NOJI*

Institute of Fisheries and Marine Biology University of Bergen
Thormøhlensgt 55, N-5008 Bergen, Norway
& Institute of Marine Research
P.O. Box 1870, N-5024 Bergen, Norway

ABSTRACT

The influence of the tube-building spionid *Polydora ciliata* Johnston on benthic community, sediment properties and exchange processes through the sediment surface was investigated. Findings showed that spionid tube lawns (eight or more tubes. $cm^{-2}$) lowered sediment stability and enhanced accumulation of suspended particles. Organic matter was selectively transported into the sediment via feeding, which enriched sediments by up to 100 %. Only a slight increase in fluid transport in the upper sediment layers was attributed to *P. ciliata*. *Polydora* tube lawns significantly increased abundance and diversity of meio- and macrofauna. Further, they increased food input to the sediments and substrate area for colonization by micro- and meiofauna. Their fecal pellets may serve as a food source for meiofauna and chemotrophs in deeper sediment layers. Hence, *Polydora ciliata*, a well known pioneer species, reconditions disturbed sediments, where it may represent a food item for benthic grazers.

RÉSUMÉ

**Influence du Polychète Spionidé tubicole *Polydora ciliata* sur les paramètres benthiques, la faune associée et les processus de transport**

On a étudié l'influence du polychète Spionidé tubicole *Polydora ciliata* Johnston sur la communauté benthique, sur les propriétés des sédiments et sur les processus d'échange à travers la surface du sédiment. Les résultats ont montré que les pelouses de tubes de spionidés (huit ou plus tubes par $cm^2$) réduisaient la stabilité du sédiment tandis qu'elles favorisaient l'accumulation des particules en suspension. De la matière organique était sélectivement transportée dans le sédiment à travers le processus de nourrissage, ce qui enrichissait le sédiment jusqu'à 100 %. Seule une faible augmentation du transport des fluides dans les sédiments superficiels a pu être attribuée à *P. ciliata*. Les pelouses de tubes de *Polydora* augmentent significativement l'abondance et la diversité de la méio- et de la macrofaune. De plus, elles augmentent l'apport de nourriture dans les sédiments et créent le substrat pour la colonisation par la micro- et méiofaune. Leurs excréments peuvent servir comme source de nourriture pour la méiofaune et les chémotrophes dans les couches profondes de sédiment. Ainsi, *P. ciliata*, espèce opportuniste bien connue, améliore les sédiments perturbés, où elle peut représenter une source de nourriture pour les

NOJI, C. I.-M., 1994. — Influence of the tube-building spionid polychaete *Polydora ciliata* on benthic parameters, associated fauna and transport processes. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 493-501. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

brouteurs benthiques.

## INTRODUCTION

Tube-building benthic organisms significantly affect processes at the sediment-water interface by their behavior, e.g. feeding, burrowing, defecation and tube irrigation (ALLER, 1978; FÉRAL, 1989; FRITHSEN & DOERING, 1986; McCALL & TEVESZ, 1982; NOJI & NOJI, 1991; RHOADS, 1974; SCHMAGER, 1988; WEINBERG & WHITLATCH, 1983; WEINBERG, 1984; WHITLATCH & ZAJAK, 1985). Tubes which protrude into the water column influence direction and speed of the laminar bottom current (CAREY, 1983; VOGEL, 1981), the sedimentation rate of sinking particles (CAREY, 1983) and sediment stability (ECKMAN *et al.*, 1981). Therefore, tube-building organisms affect associated fauna (ECKMAN & THISTLE, 1991; OLAFSSON *et al.*, 1990; REICHARDT, 1986, TRUEBLOOD, 1991, WOODIN, 1981). The extent of this influence depends upon tube diameter, density of colonization (NOWELL & CHURCH, 1979), microbial binding of the sediment surface (FAGER, 1964; ECKMAN *et al.*, 1981) and sediment structure (RHOADS *et al.*, 1978).

In Kiel Bight (western Baltic Sea) the spionid polychaete *Polydora ciliata* Johnston is one of the most important opportunistic species (KÖLMEL, 1979). After deterioration of environmental conditions *P. ciliata* can occur in high densities. Eight or more tubes per $cm^2$ sediment surface are here defined as *Polydora* tube lawns. In a study by WEIGELT (1991) a mass occurrence of opportunistic species (*Polydora* sp., *Capitella capitata*, *Diastylis rathkei*, *Harmothoe sarsi*) was used to indicate oxygen depletion.

This study concentrated on the influence of this spionid on benthic organisms, sediment parameters and transport processes through the sediment-water interface. A comparison of natural sediments from Kiel Bight with and without *Polydora* lawns addressed the following questions: 1. Does a dense tube lawn stabilize or destabilize the sediment ? 2. Do the activities of *P. ciliata* have an impact on other organisms ? 3. What is the influence on processes of fluid transport ?

## MATERIAL AND METHODS

Sediment and fauna were sampled 10 times between May and November 1987 at a fixed station (54°33´N,10°14´E) with a depth of 19 m in Kiel Bight, Baltic Sea. Sediment with and without tube lawns was collected using a Reineck grab (20 x 30cm opening). Subsamples were extracted with cylindrical Plexiglas cores of 10 cm (redox and biomass analyses) and 5 cm (meiofauna) diameter. Macrofauna was collected with a Van Veen grab (0.1 $m^2$ collecting area). Fluid transport rates in the sediment were studied in 30 cm long Plexiglas cores (10 cm in diameter) containing "artificial" sediment prepared by sieving through 500 µm mesh, incubation without aeration for 5.5 weeks and homogenization. *Polydora* was added to half the samples, and tube lawns were soon established.

In 1-cm intervals relative sediment stability using a fall cone penetrometer (Geonor AS, Oslo, EKMAN, 1947), grain size (ATTERBERG, 1905, modified) and water content (gravimetric) were measured. Relative stability was estimated from the penetration depth of a vertically falling cone which is released directly above the surface of the studied sediment layer. The measurements were conducted shipboard to avoid transport related artifacts. Redox potential was measured with a platinum Eh-electrode (Ingold. Pt-4800-M5) in 0.5 cm intervals.

For biomass analyses sediment was cut into 0.5 and 1 cm layers for intervals above and below 3 cm, respectively. five parallels for chlorophyll *a* and pheopigments (UNESCO method, JEFFREY & HUMPHREY, 1975), adenosine triphosphate (ATP ; PAMATMAT *et al.*, 1981) and organic matter (POM) (combustion at 500 °C for 24 h) were measured for respective intervals from five cores. Individuals of *P. ciliata* were randomly selected and measured for ATP.

For meiofauna analyses defined volumes of sediment from 1 cm intervals were preserved in a buffered formalin/seawater solution (4 %) with Rose Bengal (stains protoplasm). Meiofauna (> 45 µm) was extracted according to JENSEN (1983). Macrofauna was sieved (500 µm) and preserved in a buffered formalin/seawater solution (4 %). Numeration and identification of major taxa were made using a dissecting microscope.

Source : MNHN, Paris

Fluid transport (DICKE, 1986; KITLAR, 1991) in the sediment was measured using sodium bromide solution added to water above the sediment to a concentration about 50 times higher than natural. For four days water was regularly monitored for changes in concentration, after which sediments were sectioned, porosity determined and bromide concentration in the porewater measured (KREMLING, 1983).

## RESULTS

Analyses of grain size and redox potential revealed that the sediment was silty sand (SHEPARD, 1954) and became anoxic (JØRGENSEN & FENCHEL, 1974) below 1 cm depth. The data for redox potential and grain size spectra showed no related differences over time or between the sediments with and without *Polydora* lawns. For all sampling dates relative sediment stability increased with depth, reflecting an increase in sand content from about 42 to 55 % from the surface to 8 cm depth. Relative stability of sediment with tube lawns was slightly lower, i.e. the fall cone penetrated 1 to 3 mm deeper into the sediment. The porewater content generally decreased from about 60-70 % wet weight at the sediment surface to about 36 % in 6-8 cm depth; for samples with a tube lawn values were about 5-10 % higher (Fig.1). In 5.5 cm sediment depth the porewater content of the samples without a lawn are starting to be larger than the values for the samples with lawns.

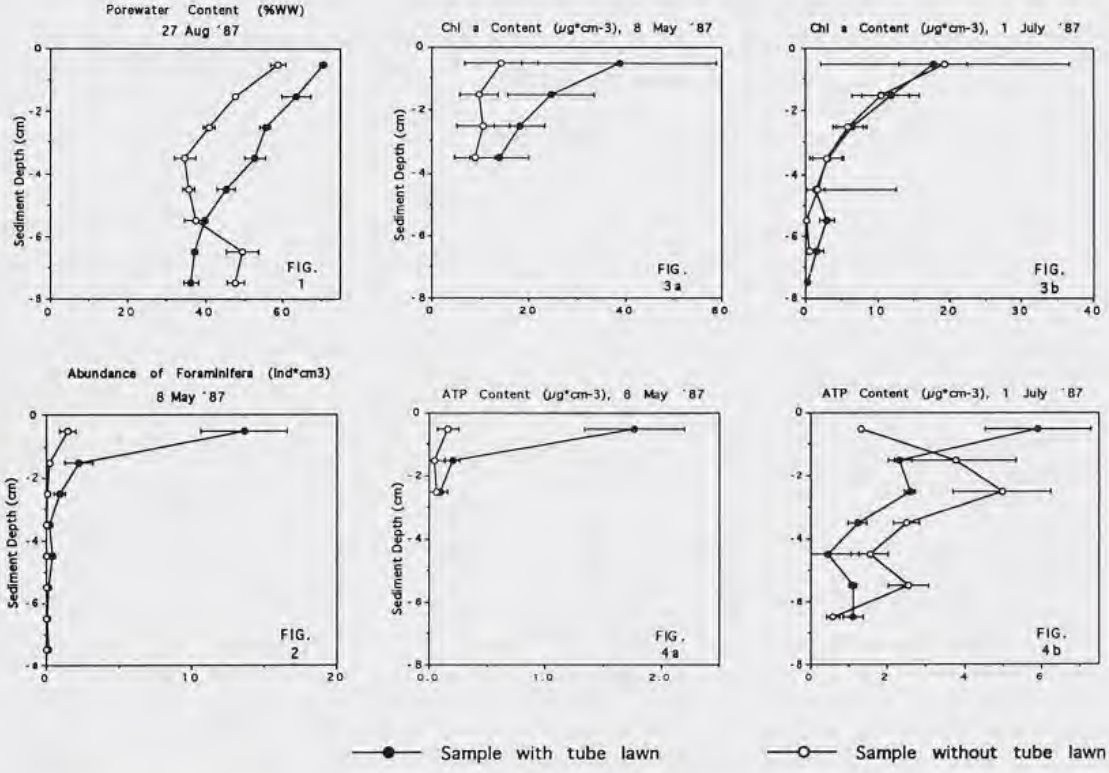



FIG. 1. — Porewater content (% of sediment wet weight (WW)) of the sediment on 27 August 1987. Mean values with standard deviations (bars) of three measurements per sediment depth layer. FIG. 2. — Abundance of foraminifera in the sediment on 8 May 1987. Mean values with standard deviations (bars) of five measurements per sediment depth layer (two measurements per depth layer below 5cm). FIG. 3. — Chlorophyll *a* content of the sediment. Mean values with standard deviations (bars) of five measurements per depth layer. (a) 8 May 1987, (b) 1 July 1987. FIG. 4. — ATP-content of the sediment. Mean values with standard deviations (bars) of five measurements per depth layer in a mixed sample. (a) 8 May 1987, (b) 1 July 1987.

Significant differences between sediments with and without lawns were found for biomass parameters in the sediment. Chlorophyll *a* content at the surface of samples with a lawn was approx. 2.5 times higher than in the sediments without a lawn on 8 May 1987 (Fig. 3a). On 1 July both sediment types had similar mean

Source : MNHN, Paris

concentrations in the surface layers (Fig. 3b). Likewise, mean ATP-concentrations in sediments with a tube lawn were 10 times higher in the surface layer (Fig. 4a). After subtraction of *Polydora*-ATP, the ATP-content in the sediments with a tube lawn was still 5.5 times higher. On 1 July the difference between the sediments was smaller, but the total ATP content had increased (Fig. 4b). The organic matter content was very similar in both sediment types on 1 July 1987, and surface values of 22-24 mg POM. $cm^{-3}$ increased to about 28mg POM. $cm^{-3}$ below 1 cm sediment depth.

The meiofauna analysis showed differences in diversities and abundances between the two sediment types. Representatives of the following groups were found: Nematoda, Harpacticida, Ostracoda, Halacarida, Turbellaria, Foraminifera, Tardigrada, larvae of Decapoda, Mollusca and Priapulida. In sediments with a tube lawn meiofauna was more diverse and 2 to 3 times more abundant than in the sediments without a lawn, i.e. 112.6 vs. 44.9 individuals. $cm^{-3}$ in the upper cm of the sediment. Corresponding differences for nematodes (84 vs. 40 ind. $cm^{-3}$ in 0-0.5 cm) and the foraminifer *Elphidium* sp. (approx. 13.6 vs. 1.5 ind. $cm^{-3}$ in 0-0.5 cm) (Fig. 2) were especially large. Regarding macrofauna, mostly juvenile organisms were found, and diversity and abundance were greater in sediments with a moderate *Polydora* population (Tab.1). Besides *Polydora ciliata* the agglutinated foraminifer *Ammotium cassis* Parker was the most common species (3519 vs. 157 ind. 0.1 $m^{-2}$ in sediments with and without a lawn, respectively). The foraminifera were located directly below or between *Polydora* tubes.

TABLE 1. — Macrofauna abundance (ind. 0.1 $m^{-2}$) in sediments with a moderate (less dense than a tube lawn) population of *P. ciliata* and with few *P. ciliata*.

| Macrofauna | With many *P. ciliata* | With few *P. ciliata* |
|---|---|---|
| Foraminifera | | |
| *Ammotium cassis* | 3519 | 157 |
| *Elphidium* sp. | 42 | |
| Priapulida | | |
| *Halicryptus spinulosus* | 18 | 3 |
| *Halicryptus* larvae | 3 | 2 |
| Bivalvia | | |
| *Mysella bidentata* | 79 | 6 |
| *Mytilus edulis* | 11 | 2 |
| *Arctica islandica* | 6 | 1 |
| *Corbula gibba* | 5 | |
| *Cerastoderma edule* | | 1 |
| Polychaeta | | |
| *Polydora ciliata* | 1142 | 22 |
| *Capitella capitata* | 91 | 20 |
| *Heteromastus filiformis* | 71 | 37 |
| *Paraonis gracilis* | 54 | 51 |
| *Harmothoe* sp. | 18 | 5 |
| *Anaitides maculata* | 9 | 3 |
| *Pectinaria koreni* | 4 | |
| *Scoloplos armiger* | 3 | |
| *Nephtys* sp. | 1 | |
| *Eteone elongata* | 1 | |
| Ostracoda | 13 | 4 |
| Malacostraca | | |
| *Diastylis rathkei* | 62 | 4 |
| TOTAL | 5152 | 318 |

Studies on fluid transport in artificial sediments showed slightly increased transport rates (0.1-0.2 mg bromide. $cm^{-3}$ in addition to molecular diffusion) down to 6cm sediment depth in the samples with a tube lawn (Fig. 5). It was assumed that the samples without tube lawn represent the pure tracer input by molecular diffusion as all

Source : MNHN, Paris

macrofauna was excluded before the experiments were started. The molecular diffusion coefficient (Ds = 5.0+/- 0.8. $10^{-6}$ cm. $s^{-1}$) is quite low compared to the coefficient in natural sediments in Kiel Bight (KITLAR, 1988).

## DISCUSSION

CHARACTERISTICS OF *POLYDORA CILIATA* JOHNSTON. — *Polydora ciliata* Johnston (body length < 30 mm) is a cosmopolitan polychaete (RAMBERG & SCHRAM, 1983) which expresses typical opportunistic life patterns especially in disturbed environments (PEARSON & ROSENBERG, 1978; RUMOHR, 1980) and reproduces nearly the whole year round with pelagic larvae (RAMBERG & SCHRAM, 1983). It is able to increase very rapidly forming spionid tube lawns. One reason for the concentrated settlement of spionid larvae next to adult individuals may be the chemosensory recognition of conspecific tubes or of chemical analogs of the tube cement (JENSEN, 1991). Video sequences from the present study site showed that *Polydora* tube lawns covered an area of 10 to 20$m^2$. Within these lawns were tubeless zones of 0.8 to 1 $m^2$ area, reasons for this colonization pattern are unknown. *P. ciliata* builds an approx. 5-cm long U-shaped tube which protrudes out of the sediment. The polychaetes either filter feed on suspended particles in the bottom water or deposit feed on sediment when the current falls below acertain speed (DAUER *et al.*, 1981; TAGHON *et al.*, 1980). Filter feeding can be important for maintenance of water quality within moderately polluted systems (DAVIES *et al.*, 1989). Filter feeding by pelagic spionid larvae can influence phytoplankton stocks (WATRAS *et al.*, 1985) via selectivity during feeding. The fecal pellets are stored in specific parts of the tube between 1 and 3 cm sediment depth (SCHÄFER, 1962).

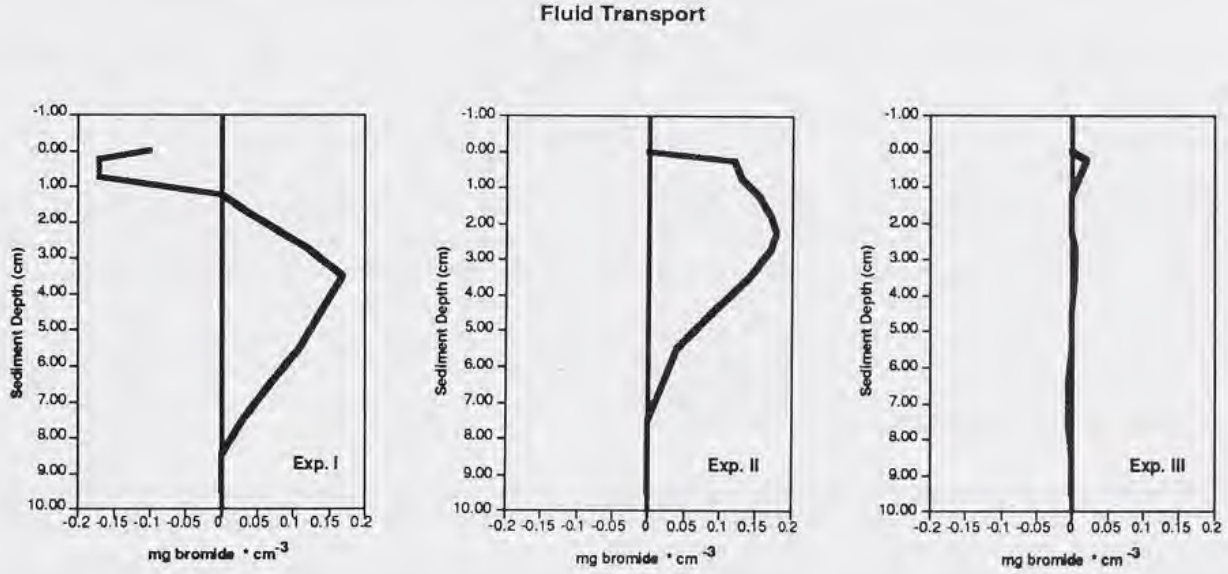



FIG. 5. — Biogenic fluid transport in artificial sediment with tube lawns measured by the concentration of bromide in the sediment pore water in three parallel experiments. (Samples without tube lawns were assumed to represent the pure tracer input by molecular diffusion. They served as base line (0-value in the graphs) in the calculations).

EFFECT ON SEDIMENTS. — Decreased relative sediment stability and higher water content are associated with burrowing, tube building, defecation and irrigation of the tubes by *P. ciliata* populations. The expected differences in grain size (FÉRAL, 1989; LUCKENBACH *et al.*, 1988) between the sediments with and without a tube lawn were not evident and could be caused by the sample treatment, as samples were treated with hydrogen peroxide to destroy organic aggregates. Redox profiles will be discussed later.

EFFECT ON BIOMASS IN THE SEDIMENT. — Differences in total biomass parameters between sediment types can be attributed to behavior and life history of *Polydora ciliata*. The 2.5-fold higher concentration of chlorophyll *a* in the samples with a *Polydora* lawn at the beginning of May may result from active suspension feeding and passive trapping of sedimenting algae by tubes protruding out of the sediment (ALLER & ALLER, 1986; BAILEY-

Source : MNHN, Paris

BROCK, 1984; CAREY, 1983). Laminar current is reduced to about 20 to 30 % on the lee side of tubes (CAREY, 1983), which accordingly, increases sedimentation rates (BUHR, 1979; WARNER, 1979). Samples with tube lawns contained approx. 50 µg chl *a* . $cm^{-3}$ more than the ones without lawns. Expressed as organic carbon ($C_{org}$ : chl *a* = approx. 40 : 1, BANSE, 1974) this additional amount of organic carbon corresponds to sedimentation during a regular spring phytoplankton bloom in this region (SMETACEK, 1980). In addition large amounts of benthic fecal pellets and flocculant detritus were trapped between the tubes. This highly concentrated organic material represented an ideal food source for other fauna. A study by YAP (1991) showed increased numbers of benthic organisms in response to greater food supply. Results of the ATP measurements and meio- and macrofauna analyses are hence not surprising. The higher meiofauna diversity and abundances down to 9 cm sediment depth in the samples with a *Polydora* lawn were presumably a result of increased amount of organic matter (ALONGI, 1985), enlarged substrate surface for meiofaunal and bacterial colonization on oxygenated tubes (BELL & COEN, 1982; BELL, 1985), and of the deep-reaching bioturbation of the more diverse and abundant macrofauna in these sediments. Large standard deviations in meiofauna abundances and diversities might be caused by patchiness in sedimented material induced by minor differences in water current and bottom topography (ECKMAN & THISTLE, 1991). Nematodes and foraminifera seemed to be best adapted to these fast-changing environmental conditions (LINKE & LUTZE, 1993). MOODLEY (1990) found for the southern North Sea that living benthic foraminifers (including *Elphidium* sp.) were enriched in areas with large amounts of organic carbon. The populations increased with rising temperature and increasing input of organic carbon. Enriched foraminifer densities were not restricted to the surface sediment but also extended into deeper sediment layers. The fact that the macrofauna was mainly comprised of juvenile organisms might be an indicator of a recent oxygen deficiency situation which had killed the benthos.

On 1 July the situation had changed. Differences in sediment biomass between the two sediment types were much smaller. During summer phytoplankton populations in the western Baltic Sea are strongly regulated by intense zooplankton grazing. This results in a large reduction of sedimenting chl *a* (SMETACEK, 1980). Consequently, no or only little additional food could be trapped between the tubes. The fresh phytoplankton material that had sedimented in May very probably was consumed by fauna within days (GRAF, 1987). This is supported by the concentration of organic matter at the sediment surface, which with 22-24 mg POM. $cm^{-3}$ was low compared to POM data at this station throughout the year (EVERSBERG, 1990). The increased sediment temperatures (8 May 1987: 3.4 °C vs. 1 July 1987 : 6.4 °C) very possibly caused the general increase in ATP-biomass in both sediment types. The difference in the degree of food input between both sediment types in May resulted in dissimilar growth rates and development of biomass. The sediments with a tube lawn showed a significant ATP maximum at the sediment surface, which may be directly associated with the tube lawns (BELL, 1985), whereas sediments without lawns were characterized by an ATP maximum below the 1-cm deep chemocline. This subsurface maximum may be due to chemoautotrophic bacteria and sulfate consumers. During periods with very little sedimentation of organic matter such a subsurface ATP maximum has been observed in other studies (GRAF, 1986, 1987).

IMPACT ON FLUID TRANSPORT RATES. — Only slightly increased fluid transport rates in the sediments with tube lawns were observed. In natural sediments of the same area KITLAR (1988) found that *Nephtys* sp., *Pectinaria koreni* Malmgren and *Halicryptus spinulosus* Von Seibold exerted a stronger influence relative to results of this study. Because of the behavior (e.g. tube irrigation) and life strategy of *P. ciliata* one would expect largely increased transport rates for fluids. In addition the surface for diffusion processes is largely increased by a dense colonization by U-shaped tubes (FOSTER-SMITH, 1978). ALLER (1983), on the other hand found that tight tubes which are coated by organic material hinder the exchange of anions because of their negatively charged tube walls. This might lead to low fluid-transport rates. This could also explain why there were no significant changes in the redox potential of the sediment. It seems that these U-shaped *P. ciliata* tubes represent a nearly closed system which allows only a minor exchange between the sediment surface and deeper sediment layers.

## ECOLOGICAL IMPLICATIONS

This study indicates that dense *P. ciliata* tube lawns can significantly improve the environmental conditions for other benthic species by loosening the sediment texture, increasing fluid transport into the sediment, increasing the concentration of easily degradable POM and enriching the diversity and abundance of benthic fauna. Therefore, in areas with disturbed sediments dense assemblages of this spionid polychaete are important as reconditioners of the

Source : MNHN, Paris

sea bottom. As the conditions in certain areas of the sea floor worsen from year to year, e.g. due to eutrophication, oxygen deficiency and trawl-fishing, animals such as *P. ciliata* become important for the re-establishment of a benthic community.

## SUMMARY

This study addresses the influence of *Polydora ciliata* on sediment properties, associated fauna and transport processes through the sediment surface. The investigation area was a 19 m deep station in Kiel Bight (western Baltic). Samples were taken from sediments with and without *Polydora* tube lawns with a box corer and grab during 10 cruises between May and November 1987. Each lawn was approximately 10 to 20 $m^2$ within which tubeless zones were present. Sediments were analyzed for redox potential, shear strength, grain sizes, porewater, particulate organic matter, chlorophyll *a*, living biomass as ATP and composition of macro- and meiofauna. In addition, experimental studies on defaunated sediments were conducted to address transport of fluids.

Relative to sediments without tube lawns the sediment stability in samples with a lawn was greater, and porewater content was lower. After sedimentation of the phytoplankton bloom in May, chlorophyll *a* and ATP concentrations were about 2.5 and 10 times higher in the sediment surface of the samples with a lawn compared with those without, respectively. In sediments with lawns, diversity and abundance of meiofauna and macrofauna were greater. Only slightly increased fluid transport rates through the sediment surface in the presence of tube lawns was observed.

The enhanced accumulation of organic matter by dense *Polydora* assemblages is a result of both the filter-feeding activity of the polychaetes and of the trapping effect of the tube. This additional food source and increased tube-related substrate area for colonization significantly improve the environmental conditions for other benthic organisms. Therefore, dense *P. ciliata* assemblages can be important as reconditioners of disturbed sediments.

## ACKNOWLEDGMENTS

I thank Dr. G. GRAF and Prof. Dr. S.A. GERLACH for critical discussions and support during the field work for this study. Also thanks to Dr. T.T. NOJI for comments on the manuscript and on the language. Dr. G. BIANCHI helped in translating the abstract into the French language.

## REFERENCES

ALLER, R.C., 1978. — Experimental studies of changes produced by deposit feeders on pore water, sediment and overlaying water chemistry. *Am. J. Sci.*, **217** : 1185-1234.

ALLER, R.C., 1983. — The importance of the diffusive permeability of animal burrow linings in determining marine sediment chemistry. *J. mar. Res.*, **41** : 299-322.

ALLER, J.Y. & ALLER, R.C., 1986. — Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. *Deep-Sea Res.*, **33** : 755-790.

ALONGI, D.M., 1985. — Microbes, meiofauna, and bacterial productivity on tubes constructed by the polychaete *Capitella capitata*. *Mar. Ecol. Progr. Ser.*, **23** : 207-208.

ATTERBERG, A., 1905. — Die rationelle Klassifikation der Sande und Kiese. *Chem. Ztg.*, **29** : 195-198.

BAILEY-BROCK, J.H., 1984. — Ecology of the tube-building polychaete *Diopatra leuckarti* Kinberg, 1865 (Onuphidae) in Hawai : Community structure, and sediment stabilizing properties. *Zool. J. Linn. Soc.*, **80** : 191-199.

BANSE, K., 1974. — On the interpretation of data for the carbon-to-nitrogen ratio of phytoplankton. *Limnol. Oceanogr.*, **19** : 695-699.

BUHR, K.-J., 1979. — Eine Massensiedlung von *Lanice conchilega* (Polychaeta: Terebellidae) im Weser-Ästuar. *Veröff. Inst. Meeresforsch. Bremerhaven*, **17** : 101-149.

BELL, S.S., 1985. — Habitat complexity of polychaete tube-caps: Influence of architecture on dynamics of a meioepibenthic assemblage. *J. Mar. Res.*, **43** : 647-671.

Source : MNHN, Paris

BELL, S.S. & COEN, L.D., 1982. — Investigations on epibenthic meiofauna. 1. Abundances on and repopulation of the tube-caps of *Diopatra cuprea* (Polychaeta: Onuphidae) in a subtropical system. *Mar. Biol.*, **67** : 303-309.

CAREY, D.A., 1983. — Particle resuspension in the benthic boundary layer induced by flow around polychaete tubes. *Can. J. Fish. Aquat. Sci.*, **40** : 301-308.

DAUER, D.M., MAYBURY, C.A. & EWING, R.M., 1981. — Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. exp. mar. Biol. Ecol.*, **54** : 21-38.

DAVIES, B.R., STUART, V. & DE VILLIERS, M., 1989. — The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* (Fauvel)) and its effects on water quality in a coastal marina. *Estuar. Coast. Shelf Sci.*, **29** : 613-620.

DICKE, M., 1986. — Vertikale Austauschkoefficienten und Porenwasserfluß an der Sediment/Wasser-Grenzfläche. *Ber. Inst. für Meereskunde an der CAU Kiel*, **155**.

ECKMAN, J.E., NOWELL, A.R.M. & JUMARS, P.A., 1981. — Sediment destabilization by animal tubes. *J. mar. Res.*, **39** (2) : 361-374.

ECKMAN, J.E. & THISTLE, D., 1991. — Effects of flow about a biologically produced structure on harpacticoid copepods in San Diego Trough. *Deep-Sea Res.*, **38** : 1397-1416.

EKMAN, S., 1947. — Über die Festigkeit der marinen Sedimente als Faktor der Tierverbreitung, ein Beitrag zur Associationsanalyse. *Zool. Bidrag. Uppsala*, **25** : 1-20.

EVERSBERG, U., 1990. — Abbau und Akkumulation von organischer Substanz in den Sedimenten der Kieler Bucht. *Ber. Inst. für Meeresforsch.*, Univ. Kiel, **193**, 1-98.

FAGER, E.W., 1964. — Marine sediments: effects of a tube-building polychaete. *Science*, **143** : 356-359.

FÉRAL, P., 1989. — Biosedimentological implications of the polychaete *Lanice conchilega* (Pallas) on the intertidal zone of two Norman sandy shores (France). *Bull. Soc. Geol. Fr.* (8 Sér.), **5** (6) : 1193-1200.

FOSTER-SMITH, R.L., 1978. - An analysis of water flow in tube-living animals. *J. exp. mar. Biol. Ecol.*, **34** : 79-95.

FRITHSEN, J.B. & DOERING, P.H., 1986. — Active enhancement of particle removal from the water column by tentaculate benthic polychaetes. *Ophelia*, **25** 169-182.

GRAF, G., 1986. — Winter inversion of biomass and activity profile in a marine sediment. *Mar. Ecol. Progr. Ser.*, **33** : 231-235.

GRAF, G., 1987. — Benthic energy flow during a simulated autumn bloom sedimentation. *Mar. Ecol. Prog. Ser.*, **39** : 23-29.

JEFFREY, S.W. & HUMPHREY, G.F., 1975. — New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.*, **167** : 191-197.

JENSEN, P., 1983. — Meiofaunal abundance and vertical zonation in a sublittoral soft bottom, with a test of the Haps corer. *Mar. Biol.*, **74** : 319-326.

JENSEN, R.A., 1991. — Bioadhesion and morphogenesis in a marine polychaete. *In*: M.-F. THOMPSON, R. SAROJINI & R. NAGABHUSHANAM (eds), *Bioactive compounds from the marine organisms with emphasis on the Indian Ocean. An Indo-United States Symposium*: 179-183.

JØRGENSEN, B.B. & FENCHEL, T., 1974. — The sulfur cycle of a marine sediment model system. *Mar. Biol.*, **24** : 189-201.

KITLAR, J., 1988. — *Leistungen verschiedener Benthostiere beim Wasseraustausch an der Grenzfläche zwischen Meer und Meeresboden*. Master's Thesis, Univ. Kiel, 68 pp.

KITLAR, J., 1991. - Der Einfluß der Bioturbation auf den Transport gelöster Stoffe im Porenwasser. *Ber. Inst. Meereskunde*, Univ. Kiel, 210, 1-99.

KÖLMEL, R., 1979. — *Ökosysteme im Wechsel zur Anaerobiose. Zoobenthos und Abbau in zeitweise anoxischen Biotopen der Kieler Bucht*. PhD. Thesis, Univ. Kiel, 304 pp.

KREMLING, K., 1983. — Determination of the major constituents. *In*: GRASHOFF, K., ERHARDT, M. & KREMLING, K. (eds.), *Methods of Seawater Analysis*, Verlag Chemie, Weinheim, 2 edition : 260-262.

LINKE, P. & LUTZE, G.F., 1993. — Microhabitat preferences of benthic foraminifera - a static concept or a dynamic adaptation to optimize food acquisition? *Mar. Micropal.*, **20** : 215-234.

Source : MNHN, Paris

LUCKENBACH, M.W., HUGGETT, D.V. & ZOBRIST, E.C., 1988. — Sediment transport, biotic modifications and selection of grain size in a surface deposit-feeder. *Estuaries*, **11** : 134-139.

MCCALL, P.L. & TEVESZ, M.J.S., 1982. — *Topics in geobiology, volume 2. Animal-sediment relations. The biogenic alteration of sediments*. Plenum Press, New York. 329 pp.

MOODLEY, L., 1990. — Southern North Sea seafloor and subsurface distribution of living benthic foraminifera. *Neth. J. Sea Res.*, **27** : 57-71.

NOJI, C.I.-M. & NOJI, T.T., 1991. — Tube lawns of spionid polychaetes and their significance for recolonization of disturbed benthic substrates: a review. *Meeresforsch.*, **33** : 235-246.

NOWELL, A.R.M. & CHURCH, M., 1979. — Turbulent flow in a depth-limited boundary layer. *J. Geophys. Res.*, **84** : 4816-4824.

OLAFSSON, E., MOORE, C.G. & BETT, B.J., 1990. — The impact of *Melinna palmata* Grube, a tube-building polychaete, on meiofaunal community structure in a soft-bottom subtidal habitat. *Estuar. coast. Shelf Sci.*, **31** : 883-893.

PAMATMAT, M.M., GRAF, G., BENGTSSON, W. & NOVAK, C.S., 1981. — Heat production, ATP concentration and electron transport activity of marine sediments. *Mar. Ecol. Progr. Ser.*, **4** : 135-143.

PEARSON, T.H., ROSENBERG, R., 1978. — Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. mar. Biol. Ann. Rev.*, **16** : 229-311.

POWILLEIT, M., 1988. — *Die Bioturbationsleistung des Priapuliden Halicryptus spinulosus in der Kieler Bucht*. Master's Thesis, Univ. Kiel, 67 pp.

RAMBERG, J.P. & SCHRAM, T.A., 1983. — A systematic review of the Oslofjord species of *Polydora* Bosc and *Pseudopolydora* Czerniavsky, with some new biological and ecological data. (Polychaeta: Spionidae). *Sarsia*.

REICHARDT, W.T., 1986. — Polychaete tube walls as zonated microhabitats for marine bacteria. *Actes Colloq. IFREMER*, **3** : 415-425.

RHOADS, D.C., MCCALL, P.L., YINGST, J.Y., 1978. — Disturbance and production on the estuarine seafloor. *Am. Sci.*, **66** : 577-586.

RHOADS, D.C., 1974. — Organism-sediment relations on the muddy sea floor. *Oceanogr. mar. Biol. Annu. Rev.*, **12** : 263-300.

RUMOHR, H., 1980. — *Der "Benthosgarten" in der Kieler Bucht - Experimente zur Bodentierökologie*. Reports SFB 95, Univ. Kiel, Vol. 55. 179 pp.

SCHÄFER, W., 1962. — *Aktuo-Paläontologie nach Studien in der Nordsee*. Kramer Verlag, 666 pp.

SCHMAGER, C., 1988. — *Einfluss rasenbildender Spioniden auf den Stoffaustausch am Meeresboden*. Master's thesis, Univ. Kiel, 64 pp.

SHEPHARD, P.E., 1954. — Nomenclature based on sand-silt-clay ratios. *J. Sedimen. Petrol.*, **24** : 151-158.

SMETACEK, V., 1980. — Annual cycle of sedimentation in relation to plankton ecology in Western Kiel Bight. *Ophelia*, suppl., **1** : 65-76.

TAGHON, G.L., NOWELL, A.R. & JUMARS, P.A., 1980. — Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science*, **210** : 562-564.

TRUEBLOOD, D.D., 1991. — Spatial and temporal effects of terebellid polychaete tubes on soft-bottom community structure in Phosphorescent Bay, Puerto Rico. *J. exp. mar. Biol. Ecol.*, **149** : 139-159.

VOGEL, S., 1981. — *Life in moving fluids. The physical biology of flow*. Willard Grant Press, Boston, 352 pp.

WARNER, G.F., 1979. — Aggregation in echimoderms. *In*: G. LARWOOD & B.R. ROSEN (eds), *Systematics Association Special Volume No. 11, Biology and Systematics of colonial organisms*. Academic Press, London & New York : 375-396.

WATRAS, C.J., GARCON, V.C., OLSON, R.J., CHRISHOLM, S.W. & ANDERSON, D.M., 1985. — The effect of zooplankton grazing on estuarine blooms of the toxic dinoflagellate *Gonyaulax tamarensis*. *J. Plankt. Res.*, **7** : 891-908.

WEIGELT, M., 1991. — Short- and long-term changes in the benthic community of the deeper parts of Kiel Bay (Western Baltic) due to oxygen depletion and eutrophication. *Meeresforsch.*, **33** : 197-224.

WEINBERG, J.R. & WHITLATCH, R.B., 1983. — Enhanced growth of a filter-feeding bivalve by a deposit-feeding polychaete by means of nutrient regeneration. *J. mar. Sci.*, **41** : 557-569.

Source : MNHN, Paris

WEINBERG, J.R., 1984. — Interactions between functional groups in soft-substrate : do species differences matter? *J. exp. mar. Biol. Ecol.*, **80** : 11-28.

WHITLATCH, R.B. & ZAJAK, R.N., 1985. — Biotic interactions among estuarine infaunal opportunistic species. *Mar. Ecol. Progr. Ser.*, **21** : 299-311.

WOODIN, S.A., 1981. — Disturbance and community structure in a shallow water sand flat. *Ecology*, **62** : 1052-1066.

YAP, H.T., 1991. — Benthic energy dynamics in a southern Baltic ecosystem. *Mar. Biol.*, **108** : 477-484.

Source : MNHN, Paris

# Patterns of abundance and diversity from the abyss - polychaetes from northeastern Atlantic abyssal plains

*Gordon L. J. PATERSON*, John D. GAGE**, P. LAMONT***
*B. J. BETT *** & M. H. THURSTON****

* The Natural History Museum, London SW7 5BD
** Scottish Marine Biological Association
PO Box 3, Oban, Argyll PA34 4AD
*** Institute of Oceanographic Sciences Deacon Laboratory
Brook Road, Wormley, Godalming, Surrey GU8 5UB, U.K.

## ABSTRACT

Preliminary results are presented from an intensive study of three abyssal plain sites in the NE Atlantic. The aim of this study was to assess the similarity of polychaete faunas from sites with different trophic characteristics. Analysis of polychaete families from the Porcupine, Madeira and Tagus abyssal plains showed differences in composition and richness. Comparisons with other deep abyssal studies provide further evidence that polychaete faunas of abyssal basins vary regionally.

## RÉSUMÉ

**Abondance et diversité des Polychètes des plaines abyssales du nord-est atlantique**

Les résultats préliminaires d'une étude intensive de trois sites des plaines abyssales de l'Atlantique nord-est sont présentés. Le but de cette étude était d'évaluer la similarité des faunes de polychètes provenant d'emplacements aux caractéristiques trophiques différentes. L'analyse de quelques familles de polychètes des plaines abyssales de Porcupine, de Madère et du Tage a montré des différences de composition et de richesse. Des comparaisons avec d'autres travaux en zone abyssale profonde apportent des preuves supplémentaires sur la variation régionale des faunes de polychètes des bassins abyssaux.

## INTRODUCTION

The abyssal plains of the world ocean represent approximately 40 % of the surface of the Earth, making them one of the largest habitats on the planet. They have been perceived as vast open, physically monotonous habitats without definable limits. However, pan-ocean studies carried out by the former Soviet Union have detected broad patterns of animal distributions (VINOGRADOVA, 1979) and have lead to general trophic classifications of the deep

PATERSON, G.L.J., GAGE, J.D., LAMONT, P., BETT, B.J. & M.H. THURSTON, 1994.— Patterns of abundance and diversity from the abyss - polychaetes from northeastern Atlantic abyssal plains. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 503-511. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

ocean fauna (SOKOLOVA, 1972). Despite these studies our understanding of the processes which operate within deep-ocean basins, and of local scales of faunal distributions, remains poor. To date there have been relatively few quantitative studies which have concentrated on a single abyssal plain site, e.g. HESSLER & JUMARS (1974, Climax site - North Pacific); KHRIPOUNOFF *et al.* (1980, Vema Fracture Zone); LAUBIER & MONNIOT (1985, Bay of Biscay); NOWELL & HOLLISTER (1985, HEBBLE, Northwestern Atlantic), SIBUET *et al.* (1984, Demerara Abyssal Plain), THIEL *et al.* (1989, BIOTRANS site - Northeastern Atlantic) and WILSON & HESSLER (1987, ECHO - N. Pacific).

In 1989, as part of a European Community Marine Science and Technology (MAST) programme, three Northeastern Atlantic abyssal plains were selected for intensive study. Each site was characterised by differences in the trophic regime. An aim of this continuing programme is to assess how differences in the physical environment, particularly nutrient flux, affect the abundance, diversity and trophic structure of the benthic populations.

We present, herein, a preliminary analysis of the polychaete fauna at these sites, concentrating on the familial similarity. We ask a basic question: are the polychaete faunas of abyssal plains dominated by the same families? Several authors have noted that nearly all polychaete families have representatives in the deep sea, e.g. ELIASON (1951) and HARTMAN (1965, 1971), but it is less clear whether certain families predominate. Answering such a question is a first step in assessing biodiversity amongst the sediment dwelling fauna of deep ocean basins.

To broaden the scope of our study, we compare our results with published data from two other deep abyssal sites, HEBBLE in the Northwestern Atlantic and ECHO in the eastern tropical Pacific.

## STUDY SITES

The three sites investigated were: Porcupine Abyssal Plain (PAP) - 48°50'N 16°30'W, c.4,850 m; Madeira Abyssal Plain (MAP) - 31°10'N 21°10'W, c.4,900m and Tagus Abyssal Plain (TAP) - 38°00'N 11°40'W, c. 5080 m. Studies on the PAP and MAP sites were initiated as part of the Institute of Oceanographic Sciences Deacon Laboratory Deepseas programme, while the Tagus was studied as part of the Scottish Marine Biological Association deep-sea benthos programme.

The PAP and MAP sites were selected to be: distant from the continental margin, of comparable depth, as representative of flat abyssal plains, and under oceanic regions exhibiting markedly different depths of winter mixing (A. L. RICE, pers. comm.). Surface productivity is somewhat greater over the PAP site than at the MAP (BERGER, 1989). Data from nearby sites suggest that PAP and MAP experience seasonal fluxes of organic matter, with lower values at MAP reflecting lower surface productivity (LAMPITT, 1992; HONJO & MANGANINI, 1993). Seasonal deposition of phytodetritus, characteristic of northeastern Atlantic waters (BILLETT *et al.*, 1983; RICE *et al.*, 1986; THIEL *et al.*, 1988/89) occurs at PAP but not at MAP (A. L. RICE, pers. comm.). TAP is a semi-enclosed abyssal basin. Overlying productivity values suggests a nutrient regime intermediate or higher than MAP and PAP (BERGER, 1989; KOBLENZ- MISHKE *et al.*, 1970). It is not known if there is a seasonal component to nutrient flux in the benthos.

There are comparable published data on the polychaete fauna from two other abyssal sites: HEBBLE (42°24'N 63°7.4W and 42°24'N 63°9.6W, 4,626 m NOWELL & HOLLISTER, 1985), which although not strictly on the abyssal plain, lies at a similar depth to our sites; and ECHO in the equatorial eastern Pacific (14°40'N: 125°25'W, c.4,500 m SPIESS *et al.* 1987). HEBBLE is subject to extreme physical disturbance which structures the community (THISTLE *et al.*, 1985) making an interesting comparison with the more quiescent NE Atlantic sites. ECHO lies in an oligotrophic to mesotrophic region of the eastern Pacific and was the site of a manganese nodule mining trial (WILSON & HESSLER, 1987). In the present comparison, data from the six control samples, collected at a distance from the trial site, were used.

## MATERIALS & METHODS

Samples from PAP and MAP were taken with a modified 0.25 $m^2$ USNEL spade box corer (SBC). Cores were sectioned into 0-1, 1-3, 3-5 and 5-10 cm layers, and washed through 1, 0.5, 0.3 and 0.25 mm sieves. One core from PAP (0.25 $m^2$) and three cores from MAP (0.75 m2) were analysed. TAP samples were taken with a vegematicmodified SBC, with the inner nine cores, each 0.01 $m^2$, processed through a 0.3 mm sieve. Five cores from TAP were analysed (0.45 $m^2$). All samples were preserved in 4 % buffered formaldehyde on the ship then

Source : MNHN, Paris

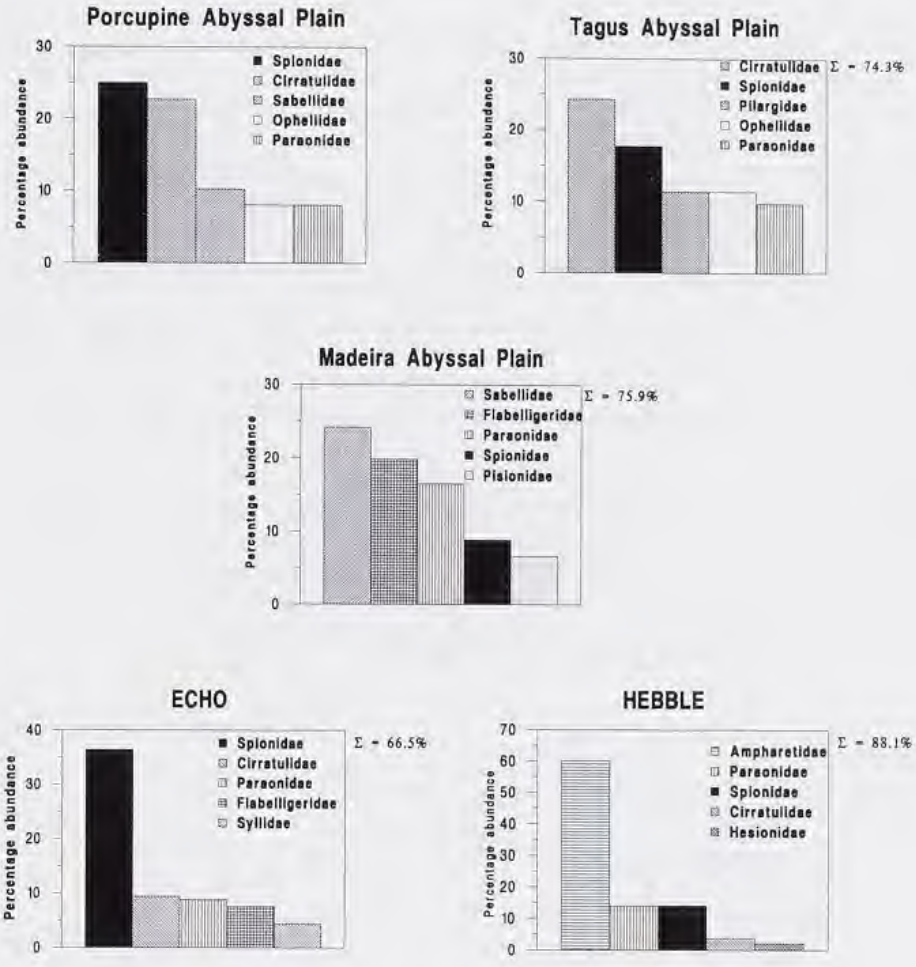



FIG. 1. — A comparison of familial abundance at each of the NE Atlantic sites studied. The five most abundant families were compared. Also shown is the familial abundances of the HEBBLE high energy site, NW Atlantic and ECHO, an equatorial eastern Pacific manganese nodule mining site. The total percentage abundance of the five dominant families is also given.

sorted and identified in the laboratory. Analyses were carried out on pooled data. The number of samples used from each site is given in figure 3. Only specimens retained on 0.3 mm sieve were used. Where more than one sieve size was used, i.e. PAP and MAP, all specimens were counted from the 0.3 mm and greater sieves. Analysis of familial similarity and richness at the different sites utilized methods which were relatively sample-size independent to avoid biases due to differences in sample abundances. Familial richness was analysed using Hurlbert rarefaction (SANDERS, 1968 - as modified by HURLBERT, 1971). Comparisons of family compositions were made using Normalised Expected Species Shared (NESS) - GRASSLE & SMITH (1976). NESS is based on the probability of the number of Operational Taxonomic Units (OTU i.e. species, trophic groups, family groups) expected to occur in common between random sub-samples drawn from the original samples. The size of the sub-sample can be determined by varying the number of individuals to be compared, m. Where m is large, upto half the size of the original sample, NESS is sensitive to the less abundant OTUs. Where m is low, NESS similarity will be based on the dominant OTUs. NESS sub-sample value, m, was set at 42 individuals. Group average clustering was used to classify the sites.

Source : MNHN, Paris

## RESULTS AND DISCUSSION

GENERAL OBSERVATIONS. — Polychaetes represented 17 % of all metazoans retained on a 0.3 mm sieve at PAP, 27 % at MAP and 25 % at TAP. These apparently low values reflect the high numbers of meiofauna, particularly nematodes and harpacticoid copepods, which were collected. If only commonly accepted macrofaunal groups are considered, then polychaetes represented 35 % of the fauna at PAP, 58 % at MAP and 49 % at TAP. Polychaetes from all the sites were generally small (c.1-5mm) and were collected primarily on the 0.3 mm sieve. Specimens appeared to be sexually immature, although most showed adult features. Large individuals were rare and were collected only in appreciable numbers by towed gears (THURSTON *et al.*, submitted).

Detailed taxonomic studies are in progress, but some initial comments can be made. Several undescribed species of *Sigambra, Aphelochaeta* and *Prionospio* appear to be present at all three sites. Species recorded from other abyssal sites, which have been found at our sites, include *Pisionura abyssorum* Hartman & Fauchald, 1971, *Aricidea tetrabranchia* Hartman & Fauchald, 1971 from the NW Atlantic, abyss and *Aurospio dibranchiata* Maciolek, 1981 from several North Atlantic deep-sea localities. Occurrence of the latter species suggests that elements of the abyssal polychaete fauna may have a wide distribution. PATERSON (1985) noted that ophiuroids from the Atlantic abyssal plains tended to have cosmopolitan distributions. However, HARTMAN (1971) estimated that fewer that 10 % of the polychaete species recorded from depths greater than 2,000m had cosmopolitan distributions.

FAMILY COMPOSITION. — None of our sites showed any marked dominance by a particular family although in common with other deep-sea sites the Spionidae, Cirratulidae and Paraonidae were common elements of the fauna. The percentage abundance of individual families differed among the three sites (Fig. 1). Spionidae and Cirratulidae were most abundant at TAP and PAP while Sabellidae and Flabelligeridae were dominant at MAP. There were variations in the other abundant families, notably the Pilargiidae (represented by one species of *Sigambra)* at TAP and Pisionidae at MAP (represented by *Pisionura abyssorum).*

The HEBBLE and ECHO sites had different compositions and less even distribution of families compared to

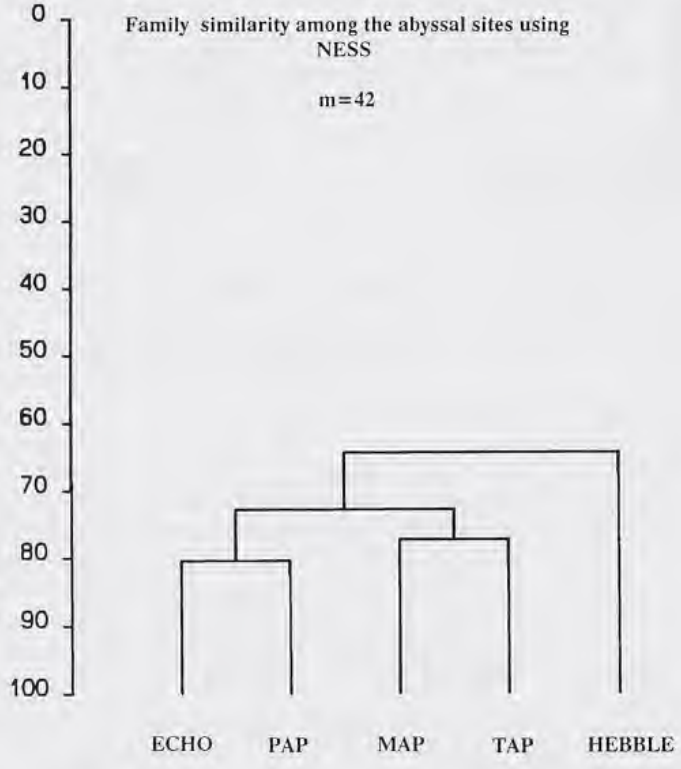



FIG. 2. — A classification of the abyssal plain sites studied using NESS similarity measure, m= 42, and clustered using group average clustering.

Source : MNHN, Paris

the NE Atlantic sites (Fig. 1). HEBBLE was dominated by one species of ampharetid accounting for c. 60 % of the macrofauna (THISTLE *et al.*, 1985), and had three of the dominant families in common with our NE Atlantic sites, whereas ECHO shared four families (WILSON & HESSLER, 1987). Familial similarity among all the sites was high as might be expected at this level of discrimination (Fig. 2). The NESS classification separated HEBBLE first. THISTLE *et al.* (1985) noted low diversity and high dominance at this site, which they linked to high disturbance. The remaining sites split into two groups: the first linked PAP and ECHO while the second grouped TAP and MAP. These groupings do not appear to reflect surface productivity. Estimates of productivity in the waters over these sites suggest ECHO would have the highest at 125 g. $Cm^{-2}$. $y^{-1}$, while PAP, TAP amd MAP have 40-60, 60-90 and 40 gC. $m^{-2}$. $y^{-1}$ respectively. However, relating composition to trophic regimes is difficult. For example, ECHO was subject to sediment resuspension due to the action of the mining equipment (WILSON & HESSLER, 1987) so it is possible that this disturbance affected the benthos in a similar way to the dramatic inputs of phytodetritus at the PAP, hence the similarity of the familial fauna between these two sites.

FAMILIAL RICHNESS. — Rarefaction curves for the different sites (Fig. 3) showed that the Tagus and Porcupine Abyssal plains had a higher diversity than Madeira Abyssal Plain. It is not possible to compare TAP and PAP directly because the curves intersect, nevertheless, it is interesting to note the high diversity of PAP from the single sample analysed to date. Despite differences in sample numbers at each site there was no correlation between sample number and numbers of families or numbers of individuals ($r^2 = 0.3$ and 0.35 respectively, d.f. = 3).It should be noted that familial diversity is not a substitute for species diversity; the species to family ratio estimated from samples currently being analysed is at least 2 : 1. So to answer our original question: the same polychaete families do not dominate the fauna although the Spionidae, Cirratulidae and Paraonidae are often among the most abundant families. Continuing studies at the species level will provide greater resolution to assess how biodiversity of polychaetes varies in different abyssal plains and how this might be linked to the trophic regime. Abyssal plains appear to differ despite their open, seemingly featureless expanses.

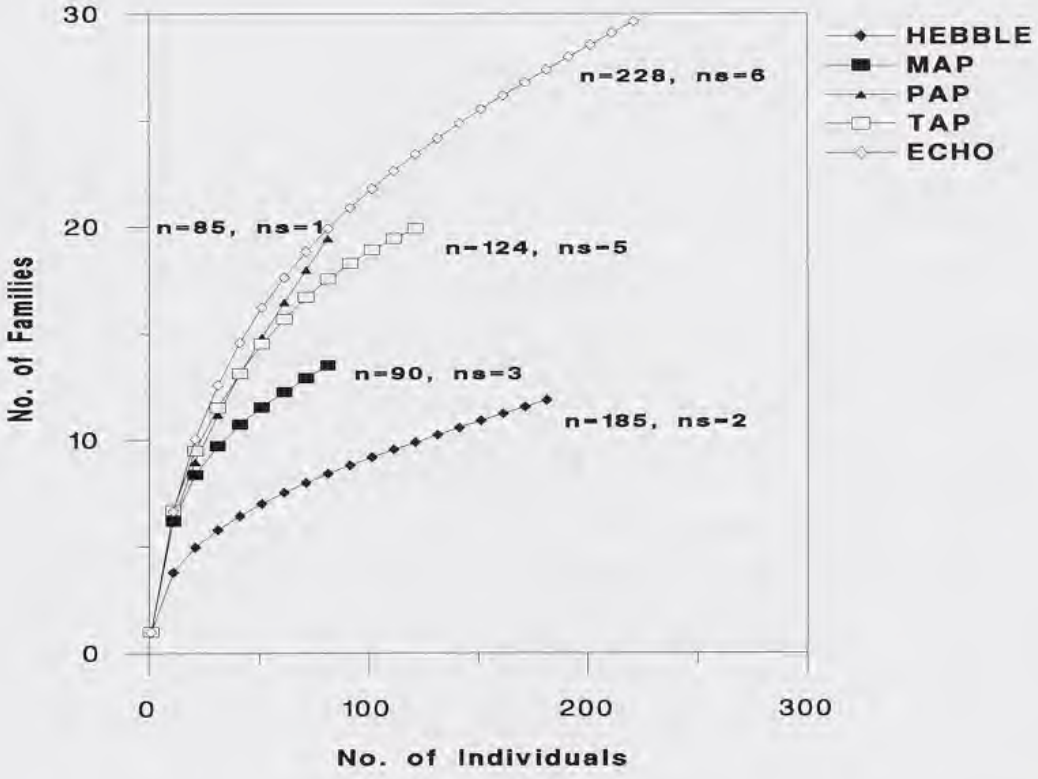



FIG. 3. — Family richness curves using rarefaction. n= total number of individuals, ns = number of samples pooled. There was no correlation between number of samples and number of families or number of individuals.

Source : MNHN, Paris

## ACKNOWLEDGEMENTS

We would like to acknowledge the support and help of the Masters, crew and scientific parties of RRS Discovery cruises 185, 186, and 194. Thanks are due to Prof David THISTLE (Florida State University) for supplying the rarefaction programme and information on the HEBBLE site, Dr Eugene GALLAGHER (University of Massachusetts) who supplied the NESS programme and Dr George D. F. WILSON (Australian Museum) for data on the ECHO site. We would also like to thank Drs John LAMBSHEAD & Tim FERRERO for commenting on the manuscript, and to Jim CHIMONIDES for computer assistance. This reseach was carried out as part of EC MAST contract 0037-C(EDB).

## REFERENCES

BERGER, W.H., 1989. — Global Ocean productivity. *In*: W.H. BERGER, V.S. SIMESTACEK & G. WEFER (eds), *Productivity of the Oceans: Past and Present*. Chichester, John Wiley & Sons : 429-455.

BILLET, D.S.M., LAMPITT, R.S., RICE, A.L., & MANTOURA, R.F.C., 1983.— Seasonal deposition of phytoplankton to deep-sea benthos. *Nature*, **303** : 520-522.

ELIASON, A., 1951. — Polychaeta. *Rep. Swed. Deep Sea Exped.*, **2** : 131-148.

GRASSLE, J.F. & SMITH, W., 1976. — A similarity measure sensitive to the contribution of rare species and its use in investigations of variation in marine benthic communities. *Oecologia*, **25** : 1322.

HARTMAN, O., 1965. — Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occ. Pap. Allan Hancock Fdn*, **28** : 1-378.

HARTMAN, O., 1971. — Abyssal polychaetous annelids from the Mozambique Basin off Southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide areas. *J. Fish. Res. Bd. Canada* ,**28** : 1407-1428.

HESSLER, R.R., & JUMARS, P.A., 1974. — Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.*, **21** : 185-209.

HONJO, S. & MANGANINI, S. J., 1993. — Annual biogenic particle fluxes to the interior of the northeast Atlantic Ocean; studies at 34°N 21° and 48°N 21°W. *Deep-Sea Research*, **40** : 587-607.

HURLBERT, S.H., 1971. — The non-concept of species diversity: a critique and alternative parameters. *Ecology*, **52** : 577-586.

KHRIPOUNOFF, A., DESBRUYÈRES, D. & CHARDY, P., 1980. — Les peuplements benthiques de la faille VEMA: données quantitatives et bilan d'énergie en milieu abyssal. *Oceanol. Acta*, **3** : 187- 198.

KOBLENZ-MISHKE, O.J., VOLKOVINSKY, V.V. & KABANOVA, J.G., 1970. — Plankton primary production of the World Ocean. *In*: W.S. WOOSTER (ed), *Scientific exploration of the South Pacific*, Washington, National Academy of Sciences : 183-193.

LAMPITT, R.S., 1992. — The contribution of deep-sea macroplankton to organic remineralisation: results from sediment traps and zooplankton studies over the Madeira Abyssal Plain. *Deep-Sea Res.*, **39A** : 221-233.

LAUBIER, L. & MONNIOT, C., 1985. — *Peuplements profonds du golfe de Gascogne*. Brest, IFREMER, 629pp.

NOWELL, A.R.M. & HOLLISTER, C.D., 1985. — Deep ocean sediment transport - preliminary resullts of the High Energy Benthic Boundary Layer Experiment. The objectives and rationale of HEBBLE. *Mar. Geol.*, **66** : 1-11.

PATERSON, G.L.J., 1985. — Deep-sea Ophiuroidea of the N. Atlantic Ocean. *Bull. Br. Mus. nat. Hist. Zool.*, **49** : 1-162.

RICE, A.L. , BILLETT, D.S.M., FRY, J., JOHN, A.W.G., LAMPITT, R.S., MANTOURA, R.F.C. & MORRIS, R.J., 1986. — Seasonal deposition of phytodetritus to the deep-sea floor. *Proc. Roy. Soc. Edinb.*, **88B** : 265-279.

SANDERS, H.L., 1968. — Marine benthic diversity: a comparative study. *Am. Nat.*,**102** : 243-282.

SIBUET, M., MONNIOT, C., DESBRUYERES, D., DINET, A., KHRIPOUNOFF, A., ROWE, G.T. & SEGONZAC, M., 1984. — Peuplements benthiques et caractéristiques trophiques du milieu dans la plaine abyssale de Demerara. *Oceanol. Acta*, **7** : 345-358.

SOKOLOVA, M.N., 1972. — Trophic structure of deep-sea macrobenthos. *Mar. Biol.*, **16** : 1-12.

SPIESS, F.N., HESSLER, R.R., WILSON, G. & WEYDERT, M., 1987. — Environmental effects of deep-sea dredging. *Scripps Institute of Oceanography Reference*, 87-5 : 1-86.

Source : MNHN, Paris

THIEL, H., PFANNKUCHE,O., SCHRIEVER, G., LOCHTE, K., GOODAY, A.J., HEMLEBEN, C.H., MANTOURA, R.F.G., TURLEY,C.M., PATCHING,J.W., RIEMAN,F., 1989. — Phytodetritus on the deep-sea floor in a central oceanic region of the NE Atlantic. *Biol. Oceanog.*, **6** : 203-239.

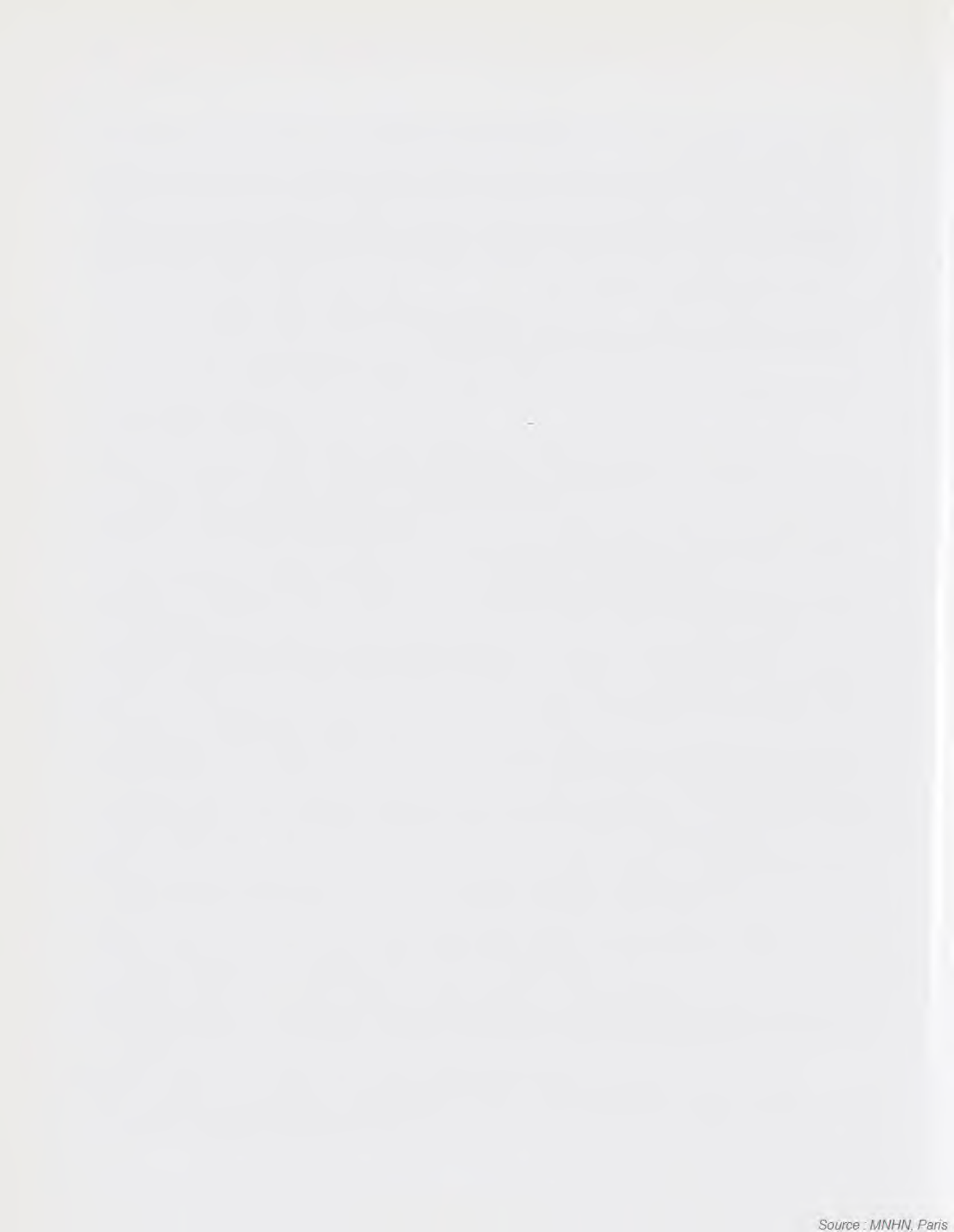
THISTLE, D., YINGST, J.Y. & FAUCHALD, K., 1985. — A deep-sea benthic community exposed to strong near-bottom currents. *Mar. Geol.*, **66** : 91-112.

THURSTON, M.H., BETT, B.J., RICE, A.L. & JACKSON, P.A.B (submitted). — Variations in invertebrate abyssal megafauna in the North Atlantic Ocean. *Deep-Sea Res.*

VINOGRADOVA, N.G., 1979. — The geographical distribution of the abyssal and hadal (ultra-abyssal) fauna in relation to vertical zonation of the ocean. *Sarsia*, **64** : 41-50.

WILSON, G & HESSLER, R.R., 1987. — The effects of manganese nodule test mining on the benthic fauna in the North Equatorial Pacific. *In*: F.N. SPIESS, R.R. HESSLER, G. WILSON & M. WEYDERT (eds). *Environmental effects of deep-sea dredging*. Scripps Institute of Oceanography Reference, 87-5 : 24-86.

Source : MNHN, Paris



Source : MNHN, Paris

# Polychaete response to different aquaculture activities

*Patricia POCKLINGTON*, David B. SCOTT*& C.T. SCHAFER***

* Centre for Marine Geology, Dalhousie University
Halifax, NS B3H 3J5, Canada
** Atlantic Geoscience Centre, Bedford Institute of Oceanography
Dartmouth, NS B2Y 4A2, Canada

ABSTRACT

The benthic macrofauna was examined at four aquaculture sites in Eastern Canada over a period of one year to determine if the heavy organic loading had a detrimental effect on the benthic communities. Two sites, one in Prince Edward Island and one in Nova Scotia, were occupied by blue mussel lines, and two sites, one in Nova Scotia and one in New Brunswick, were occupied by Atlantic salmon culture operations. Polychaete communities beneath each site plus reference sites were analyzed for comparative diversity, dominance, and the presence of indicator species such as "opportunistic" or "pioneer" species. The polychaetes which dominated the fauna beneath the mussel lines were different than those from beneath the fish cages. In both geographical locations, the sediment beneath the shellfish lines was black, finely pelletized and had high organic material content and the dominant macrofaunal organism was *Nephtys neotena*. The sediments beneath the fish cages in the New Brunswick site were black, smelled strongly of $H_2S$, had high organic material content and at times were covered with a *Beggiatoa* sp. bacterial mat. The dominant and sometimes only species was *Capitella capitata*, a species known for its tolerance to anoxic conditions and high organic enrichments. The dominant polychaete found under the fish pens at the smaller Nova Scotia site was *Nereis diversicolor*. The difference in the two fish farm sites is explained by the scale and duration of the operation. Similarly, degree of dominance at the two shellfish sites corresponds with the density of mussels and duration of operation.

RÉSUMÉ

**Réponse des polychètes à différentes activités aquacoles**

La macrofaune benthique de quatre sites d'aquaculture de l'Est du Canada a été étudiée durant une année pour déterminer si les rejets organiques avait un effet défavorable sur les communautés benthiques. Deux sites, l'un sur l'île du Prince Édouard et l'autre en Nouvelle Ecosse étaient occupés par des cordes à moules et deux autres sites, l'un en Nouvelle Écosse et l'autre dans le Nouveau Brunswick correspondaient à des fermes à saumons. Les communautés de Polychètes sous chaque site et dans des stations de référence furent analysées en terme de comparaison de la diversité, de la dominance de la présence d'espèces indicatrices telles que les "opportunistes" ou les "pionnières". Les polychètes qui dominaient la faune sous les cordes à moules étaient différentes de celles situées sous les cages à poissons. Dans les deux sites, les sédiments sous les cordes à coquillages étaient noirs, finement pélitisés et avaient une forte concentration en matière organique, l'organisme dominant était la *Nephtys*

POCKLINGTON, P., SCOTT, D.B. & C.T. SCHAFER 1994. — Polychaete response to different aquaculture activities *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 511-520. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

*neotena*. Les sédiments sous les cages à poissons dans le Nouveau Brunswick étaient noirs, avaient une forte odeur d'$H_2S$, une forte concentration en carbone organique et étaient, momentanement, recouverts d'une couche bactérienne à *Beggiaota* sp. L'espèce dominante, parfois unique, était *Capitella capitata*, connue pour sa tolérance aux conditions anoxiques et aux fortes concentrations organiques. Le polychète dominant trouvé sous les cages à poissons en Nouvelle Ecosse était *Nereis diversicolor*. La différence entre les deux fermes à poissons est expliquée par l'échelle et la durée de l'opération. De même, le degré de dominance dans les deux sites à coquillages correspond à la densité des moules et à la durée de l'exploitation.

## INTRODUCTION

One of the reported effects of sustained aquaculture activity on coastal environments is the deposition and accumulation of organic rich sediments under the aquaculture site (ANONYMOUS, 1987; GOWEN & BRADBURY, 1987; LARSSON, 1985; O'CONNOR *et al.*, 1989; PRAKASH, 1989; WESTON, 1990). A main source of organic material (OM) under shellfish lines is faeces and pseudofaeces deposited by the shellfish (KAUTSKY & EVANS, 1987). Conversely, the main source of organic material found under the fish cages at fin–fish culture sites is derived from the deposition of uneaten food in addition to the excretory products of the fish. At peak filtering time, an intensive culture of shellfish can completely filter the water contained in a bay having a volume of 548 x $10^6$ $m^3$ in seven days (DANKERS & KOELEMAIJ, 1989) and can deposit 10 kg. $m^{-2}$ of OM per annum to the sediments (TENORE *et al.*, 1982). Similarly, levels of 10 kg. $m^{-2}$ of "mixed" or multisource OM per annum (GOWEN & BRADBURY, 1987) can be deposited under a fish farm.

The consequences of the build–up of organic wastes in both types of aquaculture operations can include a change in the sedimentary regime (MATTSON & LINDEN, 1983; OTTMAN & SORNIN, 1985), an increase in oxygen consumption by the sediment (KASPAR *et al.*, 1985), formation of anoxic sediments (BROWN *et al.*, 1987) and the production and release of harmful gasses (e.g. methane, hydrogen sulphide and carbon dioxide) from the sediments to the water column (DAHLBACK and GUNNARSSON, 1981; BROWN *et al.*, 1987). These conditions can influence the structure of the benthic macrofaunal community inhabiting the affected sediments (BROWN, GOWEN, & MCCLUSKY, 1987); RITZ *et al.*, 1989; WESTON, 1990), and in severe conditions even affect the fish above (BROWN *et al.*, 1987).

It has been found that when the capacity of some sites to assimilate wastes is exceeded, it is necessary to abandon or move the installations (ROSENTHAL & RANGELEY, 1989; SORNIN, 1981; Sea Farm Canada Inc., personal comm.). A search for methods to detect the change in conditions in the environment before critical conditions develop is one of the objectives of this work. Polychaetes are widely used as indicator organisms for marine environmental quality studies (BELLAN, 1984, 1991; GLÉMAREC & HILY, 1981; see also review by POCKLINGTON & WELLS, 1992) and have been employed in this study to provide a measure of local benthic environmental impact for fin fish and shellfish aquaculture operations.

The amount of organic material in sediments under and around four aquaculture installations in eastern Canada was measured to establish that organic material was higher under the aquaculture installations than background levels. The macrobenthic community of these sediments was then examined seasonally over one year, with particular attention to the change in the polychaete fraction of the macrofauna. We wanted to determine if the effects of organic enrichment to the benthic environment from fin–fish aquaculture could be distinguished from that derived from shellfish culture activities based on the response of the polychaete community to the two types of OM loading. Quantitative approaches which have been shown to be useful in such studies such as change in diversity and degree of dominance were used. Also, we endeavoured to identify indicator species (i.e. "opportunistic" or "pioneer" species) to augment our quantitative community structure observations and to act as sentinels for monitoring environmental change between control and aquaculture sites.

## METHODS

Four aquaculture sites were monitored over one year. These include a salmon farm in the Bay of Fundy, a salmon farm with mussel lines in St. Margaret's Bay, N.S., and mussel leases in Cardigan River Estuary, P.E.I., and Lunenburg Bay, N.S. (Fig. 1). At each location, samples were taken directly under the aquaculture site, at a local reference site 25–50 m away from the aquaculture site and at reference sites 1.5–2 km away. The sites were sampled in spring, summer, fall and winter using a 225 $cm^2$ Ekman grab. Samples were sieved on a 0.5 mm mesh sieve and all benthic macrofauna was recovered and identified to the lowest taxon, counted and stored in 70 % alcohol. Sediment from all the samples was analyzed for organic carbon content based on weight loss on ignition at 500 °C for 2.5 hours.

Source : MNHN, Paris

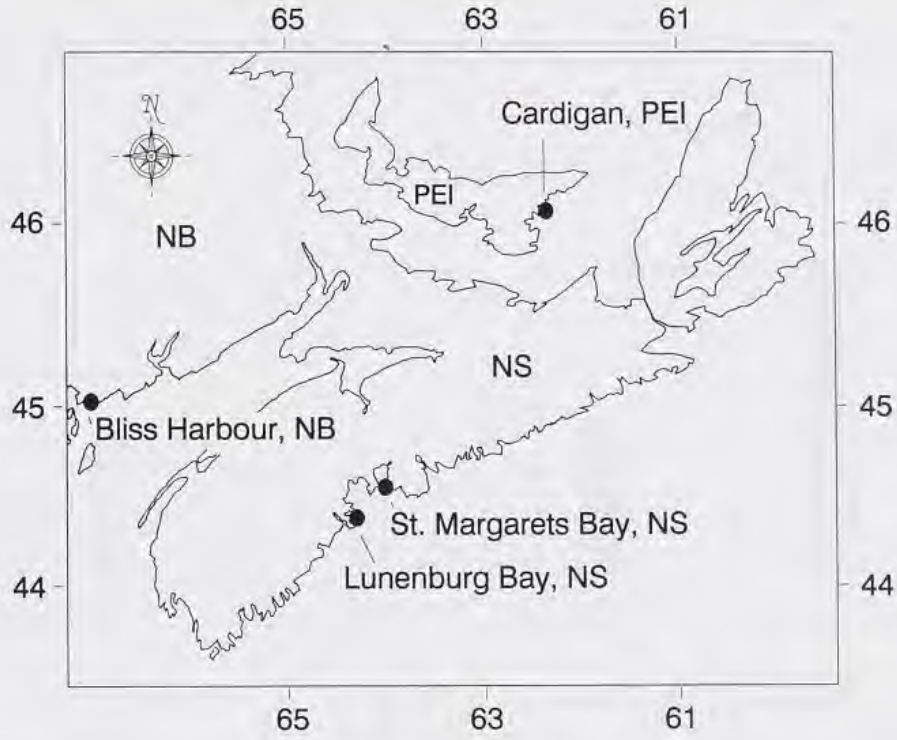



FIG. 1. — Map of eastern Canada showing location of aquaculture sites studied. PEI = Prince Edward Island; NS = Nova Scotia; NB = New Brunswick.

Polychaete macrofauna data were analyzed for diversity using the Shannon Weiner information statistic H' (SHANNON &WEAVER, 1964), dominance curves were generated by calculating cumulative per cent dominance of species (LAMBSHEAD *et al.*, 1983); in addition, the faunal lists were examined for indicator species *sensu* PEARSON &ROSENBERG (1978). All stations were subjected to cluster analysis on seasonal basis to determine natural groupings based on macrobenthic species composition. We examined these data to see if sites subjected to similar aquaculture activities were more similar than sites subjected to different aquaculture activities, or to no aquaculture activity.

## RESULTS

ORGANIC MATERIAL. — Organic material (OM) content was higher at all aquaculture sites and their closest reference sites than at their more distant reference stations (Fig. 2).

DIVERSITY. — In general, the diversity (H') of the macrofaunal community in the sediments directly beneath the aquaculture installations was lower than at the respective reference sites (Fig. 3). For example, directly beneath the fish cages in Bliss Harbour, diversity was found to be 0 in both winter and summer compared to the more distant reference site where the value of H' reached 2.2 in the winter and 2.7 in the summer. In contrast, diversities calculated for the fish farm sites in St. Margaret's Bay were relatively high in both winter and summer (H' = 1.3 and 1.1) respectively. At the 25–50 m reference sites in St. Margaret's Bay, H' ranged between 1.6 in winter and 0.56 in summer. Diversity of fauna under the shellfish lines at the Cardigan Bay location was calculated to be 0.08 in the winter and 0 in the summer with similar values at the local reference site (i.e. 0.05 and 0 respectively). Though our Cardigan Bay winter reference sample was invalid, H' for the most distant reference station in the summer was 1.07 suggesting higher diversity in summer than winter. Diversity under the mussel lines in Lunenburg Bay was slightly higher than at the near reference site in both seasons (H' = 0.9 vs 0.09 in winter and H' = 1.1 vs H' = 0.38 in summer). This is thought to be due to the increased surface area provided by the mussel lines as well as the mussels themselves which provide additional substrate for attachment by other taxa

Source : MNHN, Paris

which enhanced colonization (GRANT *et al.*, in press). Diversity at the distant reference site in Lunenburg Bay was higher than at either the mussel line or the local reference (H' = 1.55). In general, diversity is higher in winter than summer at all locations. Diversity calculated for the fish farm sites in St. Margaret's Bay were consistently higher

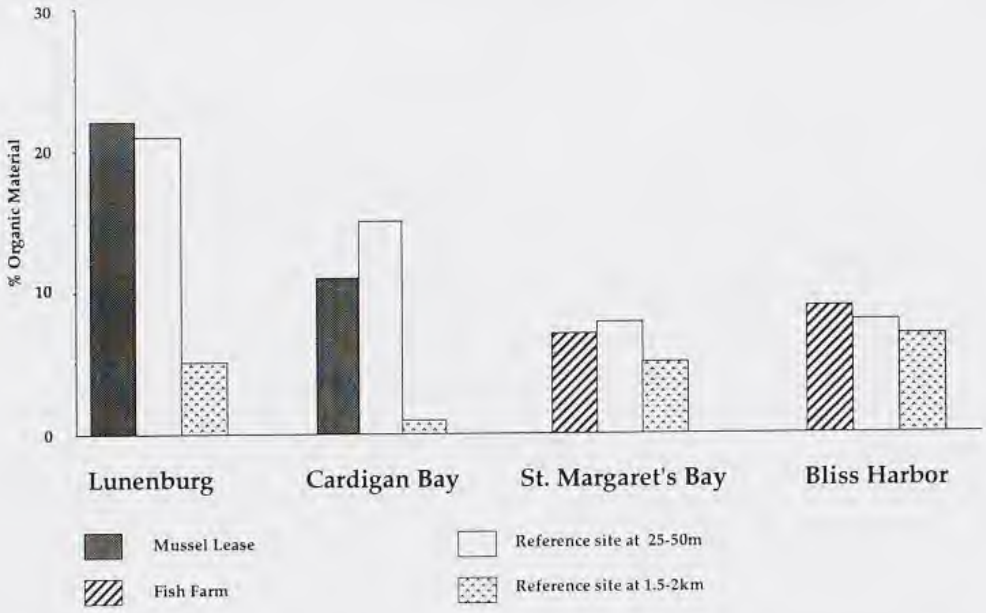



FIG. 2. — Percent organic material in sediment of site, near reference and distant reference of each aquaculture operation in summer.

than at the Bliss Harbour fin fish operation suggesting that the local impact from this installation was not as severe as at other fish farm site. As well, diversity at the mussel lease of Lunenburg Bay was higher than diversity in Cardigan Bay suggesting that the former is less impacted.

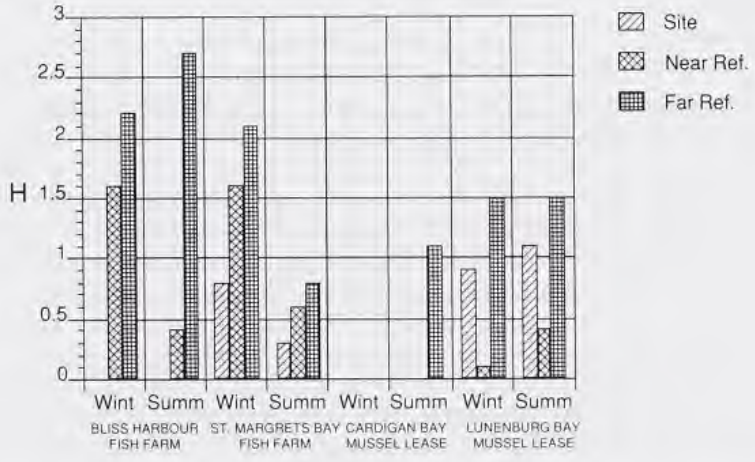



FIG. 3. — Diversity in winter and summer at the site, near reference and distant reference of each aquaculture operation. Wint = Winter; Summ = Summer.

Source : MNHN, Paris

DOMINANCE. — The dominance of the benthic community was relatively pronounced at both the fish farm and the shellfish line sites. One species accounted for, in most cases, more than half of the individuals collected at these sites. Comparative dominance curves showing per cent cumulative abundance versus species rank are given in Fig. 4 (a, b, c, d). For example, at the fish farms, when animals were found in the sediments directly under the fish cages, the percent dominance ranged from 85 to 100 % of all macrofauna collected. It is worth noting that, in Bliss Harbour, under conditions of maximum temperature in the late autumn, no macrofaunal specimens were found in the sediments. Dominance at the closest reference site was not as high as at the cage site in winter. At the

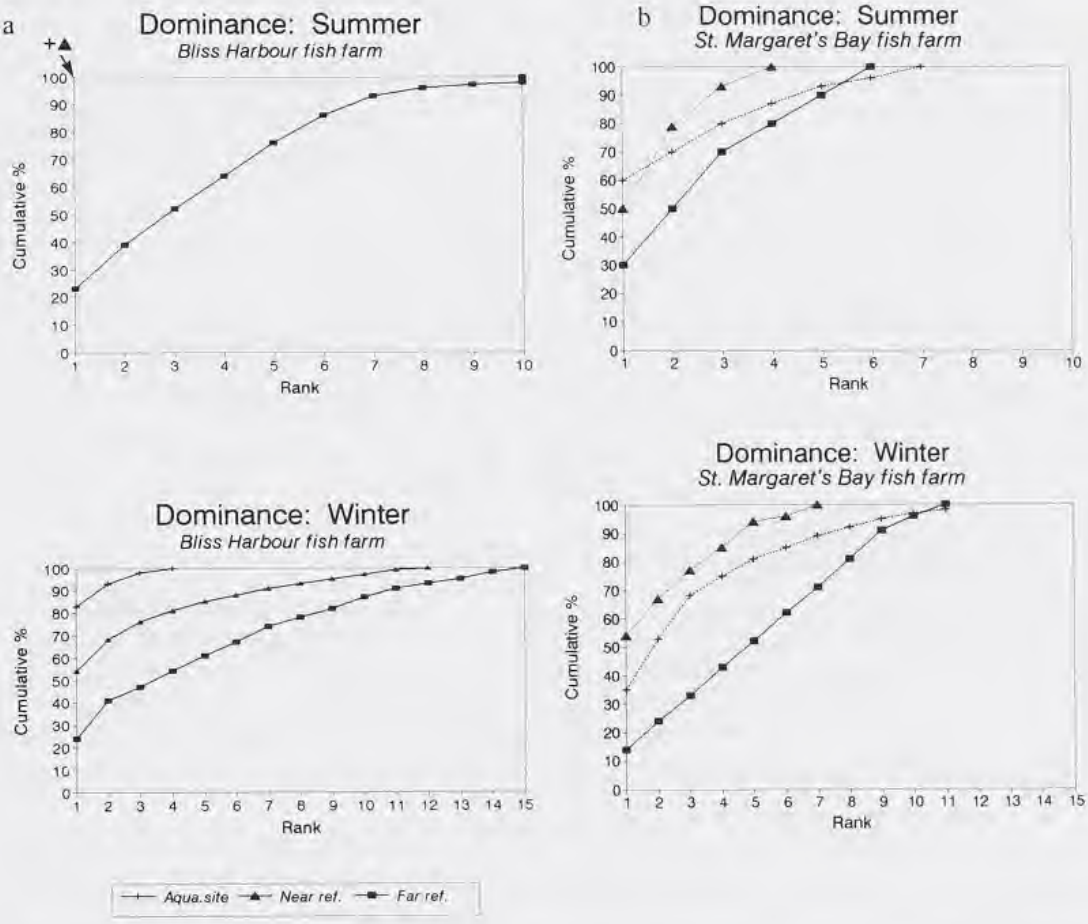



FIG. 4 a. — Dominance curve at Bliss Harbour in summer. There were no macrofaunal animals present under the fish cages in summer (August). Hence no line; only one species – *Capitella capitata* – group was collected at near reference site (30 m from fish cage), hence the * at 100 %; the cumulative abundance of species collected at the reference site 1.5–2 km away is shown. Dominance curves at Bliss Harbour in winter show greatest dodminanceoccurs at the site under fish cage (82 % of animals collected were 1 species – *Capitella capitata*) individuals collected at reference site nearest the cages are distributed over a greater number of species. At the reference site 1.5–2 km from fish cages distribution of individuals among species shows little variation from summer.

FIG. 4 b. — Dominance curves at fish cage and near reference location in St. Margaret's Bay in summer show little difference, whereas the distant reference site shows a more even distribution of individuals among species with no species accounting for more than 32 % of individuals. Dominance curve in winter similar to that in summer, animals are distributed over a greater number of species.

fish farm in St. Margaret's Bay, dominance seemed to be shared between two species (*Pholoe minuta* and *Hediste (Nereis) diversicolor*), each of which accounted for about 30 % of total number of individuals. Here, the closest

Source : MNHN, Paris

reference site was dominated by *Nereis diversicolor* but not to the same extent as under the fish cages. At the shellfish lease site in Cardigan Bay, 55–100 % of the individuals collected at both the shellfish lines and the near reference site were *Nephtys neotena*. This same species represented 31 to 63 % of the individuals collected at the mussel lease in Lunenburg Bay and 76 to 87 % of the individuals collected at the local reference site. At the more distant reference sites for most of the locations studied, no one species accounted for more than 30 % of the individuals collected.

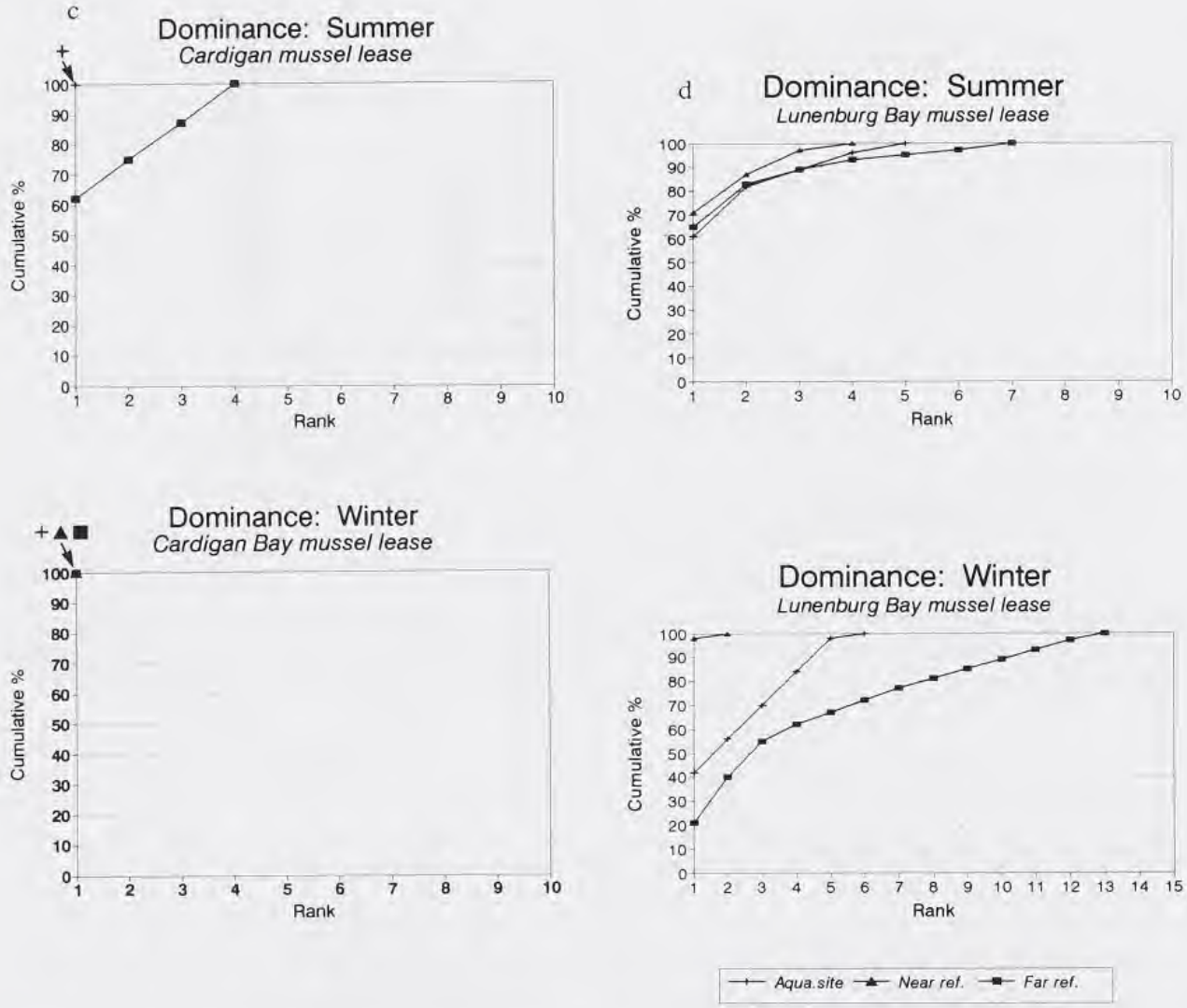



FIG. 4 c. — At Cardigan Bay in summer, the macrofauna at both mussel line and its near reference here shows 100 % comprised dominance of only one species *Nephtys neotena*. Far greater numbers at near reference site than mussel lease site. The distant reference was dominated by *Scoloplos armiger*. At Cardigan Bay in the winter, musseul lease and its near reference site only one species, *Nephtys neotena*, was collected. The distant reference site had to be discarded.

FIG. 4 d. — At Lunenburg Bay in summer, there is little difference in dominance curves between the mussel line, its near reference and its distant reference, the number of species at distance reference is greater. In winter the dominance was greatest and diversity greatest at the distant reference site.

Source : MNHN, Paris

INDICATOR ORGANISMS. — Dominant organisms under the fish cages varied with geographic location. At the late February sampling under and amongst the fish cages in Bliss Harbour, *Capitella capitata* occurred in very large numbers in all grabs (average of 11,581 ind. $m^{-2}$) and dominated the fauna, averaging 92 % of all individuals collected (range 85–98 %) under the fish cages (Fig. 5). The sediment from which they were taken was black, oozy material that smelled strongly of $H_2S$ and that was covered by a thin bacterial mat of *Beggiatoa* sp. In August, *Capitella capitata* was the only species found under the fish cages but numbers at that time were very low (44 ind. $m^{-2}$). Similarly in November, it was the dominant species found associated with sediment under the fish pens but its numbers were still relatively low (440 ind.$m^{-2}$). Away from the cages, at the local reference site faunal composition reflected a different temporal pattern. Diversity was higher and no one species represented more than 25 % of the individuals collected; this was the case during all seasons.

Though many individuals of *Capitella capitata* were found in the sediments under the fish pens at St. Margaret's Bay, this species was not the dominant taxon at this location. For example, in July, amphipod crustaceans of a surface dwelling and scavenging feeding type were the dominant organism of the benthic macrofauna under the pens and also at a reference site 20 m from the pens. It was noted that a considerable amount of algae and eel grass was collected at both of these sites. In August, however, a small scavenging polychaete *Pholoe minuta* shared dominance with *H. diversicolor* at a site amongst the cages while another site under the cages contained no macrofaunal animals whatsoever. Inshore of the cages, *H. diversicolor* was the dominant species, but in subjacent offshore environments benthic community diversity was higher and different species dominated. In November (the winter sampling), the dominant taxon under the cages was *H. diversicolor*, while away from the fish pens, the distribution of individuals among species was comparatively uniform with no one species dominant.

The dominant organism at the shellfish sites of both Lunenburg Bay and Cardigan Bay in all seasons was usually a small nephtyid, *Nephtys neotena*. However, there were exceptions. One exception occurred in November (winter) under the mussel line in Lunenburg Bay. At that time *Capitella capitata* was the dominant species comprising 42 % of all individuals (it should be noted that number of species and individuals at the Lunenburg Bay site was relatively low in winter). The other exception occurred in Cardigan Bay, in the spring, when *Nephtys neotena* was superceeded by a spionid polychaete, *Polydora socialis* which comprised 55 % of the individuals collected. *Nephtys neotena* was dominant both under the mussel lines and at the reference sites suggesting that the reference site was not far enough away from the experimental site. Dominance was also higher at the reference site than under the mussel lines in Lunenburg Bay. More distant reference stations from other parts of Lunenburg Bay did not contain representatives of *N. neotena*. At Cardigan Bay, the percent dominance was approximately the same at both the shellfish line and the reference site. A more diverse fauna was observed at the distant reference site in Cardigan Bay with several of the species collected being characteristic of fine–grained organic–rich sediments found in estuaries (e.g. *Scoloplos armiger, Lumbrineris* sp. and *Eteone* sp.).

## DISCUSSION

Under the fish cages in Bliss Harbour, the polychaetes most frequently associated with severely deteriorated conditions, *Capitella capitata*, prevailed. Large numbers of small specimens of this species were collected. Larvae of this species are known to use sulphur dioxide as a settlement cue (CUOMO, 1985). One reason this species may withstand the conditions that have developed in the aquaculture site sediments is thought to be the ability of females to build a membranous tube in which to incubate eggs which we interpret as a means of keeping the developing eggs from direct contact with the sediments. *Capitella capitata*, on the other hand, was only occasionally found associated with the shellfish leases. A different species, *Nephtys neotena*, appears to be an indicator of organic enrichment from biodeposition at shellfish line sites. Like *Capitella capitata*, it is a small burrowing, deposit–feeding species which can occur in very large numbers to the exclusion of other species in sites of organic enrichment. Though many species of the genus *Nephtys* are aggressive carnivores, the stomach contents of *Nephtys neotena* was examined whenever it was encountered and found to contain only fluidized detrital particles, suggesting a deposit–feeding mode of nutrition. Furthermore, the presence of external branchiae on this species (and not on *Capitella capitata*) suggests that it requires the presence of some oxygen in the sediment for respiratory purposes. The environmental interpretation based on this evidence is that though the levels of organic material in the sediments under the shellfish leases are very high, they do not become as anoxic as quickly as at the fish sites.

In general, the impact of aquaculture activities in Nova Scotia (both fish farms and mussel leases) appears to be less than similar activities in New Brunswick and Prince Edward Island. It seems that a mix of natural and

Source : MNHN, Paris

anthropogenic factors are involved in determining the degree of impact of an aquaculture operation on the local marine environment. One must consider the physical setting. The two Nova Scotian sites are located in bays having relatively unrestricted exchange with the Atlantic. Studies have shown that complete flushing of both St. Margaret's Bay and Lunenburg Bay can occur in a matter of 2 to 2–1/2 days (SHARAF *et al*, 1970; M. DOWD, pers. comm.). However, the Lunenburg Bay site had a causeway emplacement 20 years ago which has affected circulation in the location of the shellfish lines. Cardigan Bay, on the other hand, is a low energy way environment most of the summer, there is a greater exchange of water in the system during storms in the autumn (DRINKWATER & PETRIE, 1988; T. SEPHTON, pers. comm.). In winter, the ice cover in Cardigan Bay prevents wave–generated flushing. In Bliss Harbour, on the L'Etang Inlet of the Bay of Fundy, though the tidal range generally is relatively vigorous, there is only partial flushing of bays and inlets in this system (R. TRITES, pers. comm.), a condition which could contribute to the uninterrupted flux of organic material. Temperature range at the Nova Scotia sites are different from the other two sites. For example, maximum temperature in Lunenburg Bay is 22 °C and minimum temperature is –1.5 °C (A. HATCHER, pers. comm.). St. Margaret's Bay is similar except the lower end temperature never reaches below –0.5 °C (SHARAF *et al*, 1970). Maximum temperature in Bliss Harbour is about 14 °C while minimum to date is +2 °C (R. TRITES, pers. comm.). No precise data were available for Cardigan Bay but temperatures can get as high as +26 °C and below 0 °C in the winter (T. SEPHTON, pers. comm.) and it is an environment in which species with southern affinities are found (FOURNIER & POCKLINGTON, 1984; POCKLINGTON & TREMBLAY, 1987). Cardigan Bay also has had a causeway emplacement in the last 30 years that affects circulation in the area of aquaculture.

Along with contrasts in the rate and extent of flushing of the sites, there are other differences. One of these is density of organisms cultured and the length of time the installations have been in place. The Nova Scotian sites are much smaller and much more recent operations than the Bay of Fundy and Cardigan Bay sites. For example, there are an estimated 40,000 fish in the St. Margaret's bay operation whereas the fish farm in Bliss Harbour is about 10 times larger. Similarly, there is one mussel lease operating in the Lunenburg Bay site whereas, at last report, 10 leases were in operation in Cardigan Bay each with an estimated 35 x $10^6$ mussels per lease (T. SEPHTON & S. BATES, pers. comm.). All of these factors can contribute to the observed differences in impact on the local fauna that we have observed, together with causeway emplacements.

## CONCLUSION

Analysis of the benthic macrofauna suggests that fish farms in Bliss Harbour have a greater impact on the environment than the fish farm in St. Margaret's Bay. Low diversity and dominance by large numbers of *Capitella capitata* and the occurrence of a *Beggiatoa* sp. bacterial mat indicate that the Bliss Harbour sediments are severely impacted locally as a result of high organic loadings from the fish pens compounded by increased bacterial activity due to the lack of aeration of the sediments by flushing. The shellfish lines at the Cardigan Bay and Lunenburg Bay locations have less negative impact than the fish pens at Bliss Harbour. Sediments under and adjacent to the mussel lines continue to support populations of the small, relatively oxygen dependent, deposit feeding species (*Nephtys neotena*) which is commonly associated with the fine sediments having a high organic content. *N. neotena* is typical of estuarine environments and is common in the organic enriched and relatively fine sediments found in these nearshore settings. The occurrence suggests that, under worst case scenarios, given their location and natural setting, the impact of shellfish lines is not as deleterious as that of the fish farms.

Benthic macrofauna are useful organisms for monitoring the impact of aquaculture operations on the marine environment, and they also appear to be helpful in defining the stage of degradation. It appears that more severely impacted environments have a characteristic fauna which shows anomalous dominance and low diversity.

## ACKNOWLEDGEMENTS

The authors gratefully acknowledge Eric COLLINS, Annamarie HATCHER, Craig EMMERSON, John GRANT of Dalhousie University, and Roger POCKLINGTON, PCS, Bedford Institute of Oceanography, for their help producing figures for the manuscript, and T. SEPHTON, C. BRYANT (Dept. of Fisheries, Canada), Chloe YOUNGER and Tom DUFFETT (Dalhousie) for help in the field and organic material determinations. We also thank Paul KEIZER and Bill SILVERT of the Habitat Ecology Laboratory, Bedford Institute of Oceanography. Thanks also to the anonymous reviewers.

Source : MNHN, Paris

## REFERENCES


ANONYMOUS, 1987. — Cage pollution equals sewage. *Fish Farmer*, **10** : 24.

BELLAN, G., 1984. — Indicateurs biologiques dans le milieu marin. *Bull. Ecol.* , **15** : 13–20.

BELLAN, G., 1991. — Characteristic, indicative and sentinel species: from the conception to the utilization. *In*: O. RAVENA (ed), *Terrestrial and aquatic ecosystems: Perturbations and Recovery*, Ellis Horwood Lim., Publ., **1**(9) : 95-100.

BROWN, J.R., GOWEN, R.J. & MCCLUSKY, D.S., 1987. — The effect of salmon farming on the benthos of a Scottish sea loch. *J. exp. mar. Biol. Ecol.*, **109** : 39–51.

CUOMO, M.C., 1985. — Sulphide as a larval settlement cue for *Capitella* sp. I. *Biogeochemistry*, **1**: 169–181.

DAHLBACK, B. & GUNNARSSON, A.H., 1981. — Sedimentation and sulphate reduction under a mussel culture. *Mar. Biol.*, **6** : 269–275.

DANKERS, N. & K. KOELEMAIJ, 1989. — Variations in the mussel population of the Dutch Wadden Sea in relation to monitoring of other ecological parameters. *Helgolander Meeres.*, **43** : 529–535.

DRINKWATER, K. & PETRIE, B., 1988. — Physical oceanographic observations in the Cardigan Bay region of Prince Edward Island. 1982–1987. *Can. Tech. Rep. Hydrogr. Ocean Sci.* **110** : IV + 37 pp.

FOURNIER, J.A. & POCKLINGTON, P., 1984. — The sublittoral polychaete fauna of the Brasd'Or Lakes, Nova Scotia. *In*: P.A. HUTCHINGS (ed), *Proceedings of the First International Polychaete Conference*, Sydney. Published by the Linnean Society of New South Wales : 254–278.

GLÉMAREC, M. & HILY, C., 1981. — Perturbations apportées à la macrofaune benthique de la baie de Concarneau par les effluents urbains et portuaires. *Acta oecol., Oecol. applic.*, **2** : 139–150.

GOWEN, R.J. & BRADBURY, N.B., 1987. — The ecological impact of salmonid farming in coastal waters: A Review. *Oceanogr. mar. Biol. Ann. Revi.*, **25** : 563–575.

GRANT, J., HATCHER, A., SCOTT, DB, POCKLINGTON, P., SCHAFER, C.T. & WINTERS, G.V., in press. — A multidisciplinary approach to evaluating benthic impacts of shellfish aquaculture. *Estuaries*.

KAUTSKY, N. & EVANS, S., 1987. — Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Mar. Ecol. Prog. Ser.*, **38** : 201–212.

KASPAR, H.F., GILLESPIE, P.A., BOYER , I.C. & MACKENZIE, A.L., 1985. — Effects of mussel aquaculture on the nitrogen cycle and benthic communities in Kenepur Sound, Marlborough Sounds, New Zealand. *Mar. Biol.*, **85** : 127–136.

LAMBSHEAD, P.J.D., PLATT , H.M., & SHAW, K.M., 1983. — The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *J. Nat. Hist.*, **1** : 859–874.

LARSSON, A.M., 1985. – Blue mussel sea farming — effects on water quality. *Vatten/Water* , **41** : 218–224.

MATTSSON, J. & LINDEN, O., 1983. – Benthic macrofaunal succession under mussels, *Mytilus edulis* L. (Bivalvia). *Sarsia*, **68** : 97–102.

O'CONNOR, B.D.S., J. COSTELLAE, J., KEEGAN, B.F. & RHOADS, D.C., 1989. — The use of REMOTS technology in monitoring coastal enrichment resulting from mariculture. *Mar. Poll. Bull.*, **20**(8) : 384–390.

OTTMAN, F. & SORNIN, J.M. 1985. — Observations on sediment accumulations as a result of mollusk culture systems in France. *Proc. SIUBC VI* : 329–346.

PEARSON, T.H. & ROSENBERG, R., 1978. — Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and marine Biology Annual Review*, **16** : 229–311.

POCKLINGTON, P. & TREMBLAY, M.J., 1987. — Faunal zones in the northwestern Atlantic based on polychaete distribution. *Can. J. Zool.*, **65** : 391–402.

POCKLINGTON, P. & P.G. WELLS, 1992. — Polychaetes : key taxa for marine environmental quality monitoring. *Mar. Pollut. Bull.*, **24** : 593–598.

PRAKASH, A., 1989. — Environmental implications of coastal aquaculture. *Bulletin (A.A.C.)* . Sept. : 109–111.

RITZ, D.A., LEWIS, M.E. & SKEN, M.A.,1989. — Response to organic enrichment of infaunal macrobenthic communities under salmonid sea cages. *Mar. Biol.*, **103** : 211–214.


Source : MNHN, Paris

ROSENTHAL, H. & RANGELEY, R.W., 1989. — The effect of a salmon cage culture on the benthic community in a largely enclosed bay (Dark Harbour, Grand Mannan Island, N.B., Canada). *ICES 1989/F*, **23** : 1–17.

SHANNON, C.E. & EAVER, W.W., 1964. — *The mathematical theory of communication*. University of Illinois Press. Urbana, Ill, 125 pp.

SHARAF EL DIN, S.H., HASSAM, E.M. & TRITES, R.W., 1970. — The physical oceanography of St. Margaret's Bay. *Fish. Res. Brd Canada*. Tech. Rep., **219**, 241.

SORNIN, J.M., 1981. — Influences des installations conchylicoles sur l'hydrologie et sur lamorphologie des fonds. *Rev. Trav. Pêches marit. Nantes* , **45** : 127–139.

TENORE, K.R., BOYER, L.F., CAL, R.M., CORRAL, J., GARCIA FERNANDEZ, G., GONZALEZ–GURRIARAN, N., HANSON, R.B., IGLESIAS, I., KROM, M., E. LOPEZ–JAMA, E, MCLAIR, R.J., PAMATMAT, M.M., PEREZ, A., RHOADS, D.C., DE SANTIAGO, G., TIETJEN, J., WESTRICH , J. & WINDOM, H.L., 1982. — Coastal upwelling in the Rias Bajas, n.w. Spain, contrasting the benthic regimes of the Rias de Arosa and de Muros. *J. mar. Res.*, **40** : 701–722.

WESTON, D.P. 1990. — Quantitative examination of macrobenthic community changes along an organic enrichment gradient. *Mar. Ecol. Prog. Ser.*, **61** : 233–244.

Source : MNHN, Paris

# Influence of temperature and diet on the larval development and growth of juveniles *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae)

*Daniela PREVEDELLI*

Dipartimento di Biologia Animale, Università di Modena
Via Università 4, I-41100 Modena, Italy

ABSTRACT

The effects of temperature and food type on development and growth rate of the eunicid polychaete *Marphysa sanguinea* have been investigated under controlled laboratory conditions from the beginning of the larval feeding. Development and growth rate was evaluated under vegetarian diet (filamentous green algae), meat diet (Liebig meat extract and Gerber meat homogenates), and mixed diet containing both the two previous foodstuffs. Each diet was tested at five temperatures (13 °C, 18 °C, 24 °C, 27 °C, and 30 °C). Development and growth rate was influenced both by diet and temperature.

RÉSUMÉ

**Influence de la température et du régime alimentaire sur le développement larvaire et la croissance de *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae)**

Les effets de la température et du régime alimentaire sur le développement larvaire et sur la croissance du polychète *Marphysa sanguinea* ont été étudiés en conditions controlées au laboratoire à partir du moment où les larves commencent à s'alimenter. Le développement et la croissance ont été comparées en nourrissant les larves avec un aliment végétal (algues vertes filamenteuses), de la viande (extrait de viande Liebig et viande Gerber homogénéisé) et avec un aliment mixte composé d'algues et de viande. Chaque type d'aliment a été testé à cinq températures (13 °C, 18 °C, 24 °C, 27 °C, et 30 °C). Le développement larvaire et la croissance ont été influencés par la nature de l'aliment et la température.

## INTRODUCTION

Environmental factors strongly affect all phases of the life cycles of many marine invertebrates living in temperate waters. Temperature, photoperiod, dissolved oxygen, food quantity and composition, and salinity are among the principle environmental factors influencing seasonal cycles of reproduction, development and growth. Among these, temperature and food availability, which influence individual development, growth rates and

PREVEDELLI, D., 1994. — Influence of temperature and diet on the larval development and growth of juveniles *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 521-526. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

survivorship, are essential in determining population dynamics (BHAUD, 1988; MARSH & TENORE, 1990) and consequently the structure of marine benthic communities (RHOADS & YOUNG, 1970 ; WHITLATCH, 1980, 1981).

The role of temperature and food type on development and growth rate has been extensively investigated for "opportunistic" polychaetes with short life spans, of the order of months, short generation times, and semi-continuous reproduction, such as Capitellidae (TENORE, 1977, 1983; TENORE & CHESNEY, 1985; MARSH *et al.*, 1989; MARSH & TENORE, 1990) and Spionidae (WIBLE, 1984; LEVIN & CREED, 1986; ZAJAC, 1986; CHU & LEVIN, 1989). Only few studies have investigated the influence of environmental parameters on polychaetes defined as "equilibrium" species with longer life spans, of the order of years, slow development and fewer reproductive periods per unit time (IVLEVA, 1970; NEUHOFF, 1979; BHAUD, 1988; PREVEDELLI, 1991, 1992).

The eunicid *Marphysa sanguinea* exhibits all the characteristics of an "equilibrium" species according to the definitions of GRASSLE & GRASSLE (1974), McCALL (1977), and ZAJAC & WHITLATCH (1989). Along the Italian coast, *M. sanguinea* is very abundant in the Lagoon of Venice, a polyhaline lagoon with limited fluctuations in salinity but large seasonal changes in temperature. This species is considered to be omnivorous (DAY, 1967; FAUCHALD & JUMARS, 1979); indeed the availability of both plant and animal food source in the Venice Lagoon is very high.

The present paper is a part of a study of the life-history of *M. sanguinea* to elucidate the life-history traits adopted by this polychaete for the colonization and survival in brackish waters (PREVEDELLI, 1989). In the Venice Lagoon temperature fluctuations is the main source of environmental instability while the variety of potential food type is always high. It is therefore of interest to conduct an experimental study on the effects of temperature and diet on the development and growth of this species.

## MATERIALS AND METHODS

FIELD COLLECTIONS. — Bottom samples were collected from the Lagoon of Venice in February 1988 about two months before spawning. Adult specimens of *M. sanguinea* were extracted by hand from mud immediately after collection.

REPRODUCTION. — In the laboratory the worms were placed in tanks containing filtered lagoon mud and lagoon water under constant oxygenation. The mud was screened through a 0.5 mm sieve to remove algae, mollusc shells etc. Salinity was maintained around 30 P.S.U., which corresponded to the collection site. The tanks were maintained at 24 °C and 12/12 light/dark photoperiod. Fertilization occurred after about 30 days.

GAMETE EMISSION AND GROWTH EXPERIMENTS. — Thirty larvae of five setigerous segments just beginning to feed (20 days old) were used to study the development and growth rate in relation to temperature and diet. They were placed in 15 small glass tanks with 30 ml of filtered lagoon water and maintained at five different temperatures (13, 18, 24, 27 and 30 °C) with constant 12/12 light/dark photoperiod. The 13 - 30 °C temperature limits adopted, slighty exceed the lower and upper lagoonal water temperatures during larval emergences. The salinity was kept around 30 P.S.U. Larvae were fed with vegetarian, carnivorous and mixed diets at each tested temperature. The vegetarian diet consisted of filamentous green algae reared in the laboratory. The meat diet consisted of Liebig meat extract (0.1 g in 50 ml of distilled water) integrated with meat homogenates. The mixed diet contained both of these foods. Food was always given in abundance but food excess was avoided to prevent water anoxia. Water was changed twice a week and glass tanks were replaced with clean ones every month. Somatic growth was recorded weekly by counting the number of setigerous segments.

STATISTICAL ANALYSIS. — The SPSS (NIE *et al.*, 1975) software package was used for statistical calculations. Effects of food type and temperature regime were analyzed using a two-way analysis of variance (ANOVA). When the ANOVA showed treatment differences to be significant ($p < 0.05$), the treatment means were analyzed by an *a posteriori* Least Significant Difference (LSD) test.

## RESULTS

Experimental results are reported in table 1 and figure 1.

Source : MNHN, Paris

TABLE 1. — Mean length (number of setigers) of *Marphysa sanguinea* at each treatment (in brackets standard deviation).

| TREATMENT | | DAYS | | | | |
|---|---|---|---|---|---|---|
| | | 15 | 45 | 75 | 105 | 135 |
| 13 °C | algae | 5 (0.00) | 5 (0.27) | 6 (0.00) | 6 (0.00) | 6 (0.00) |
| | mixed | 5 (0.32) | 5 (0.35) | 6 (0.00) | 6 (0.00) | 6 (0.00) |
| | meat | 5 (0.25) | 5 (0.23) | 6 (0.00) | 6 (0.00) | 6 (0.00) |
| 18 °C | algae | 5 (0.47) | 7 (1.41) | 8 (0.95) | 13 (3.59) | 18 (3.87) |
| | mixed | 5 (0.50) | 5 (0.49) | 10 (1.40) | 11 (2.60) | 15 (2.80) |
| | meat | 5 (0.48) | 6 (0.98) | 11 (2.40) | 18 (5.40) | 23 (3.54) |
| 24 °C | algae | 5 (0.25) | 6 (0.49) | 12 (2.82) | 15 - | 26 - |
| | mixed | 5 (0.39) | 9 (1.67) | 18 (7.03) | 31 (20.50) | 36 (24.00) |
| | meat | 6 (0.81) | 11 (2.45) | 14 (4.13) | 26 (16.26) | 45 - |
| 27 °C | algae | 5 (0.21) | 7 (2.26) | 18 (4.76) | 24 (6.24) | 35 - |
| | mixed | 6 (0.82) | 12 (3.34) | 17 (5.34) | 25 (6.41) | 30 (2.12) |
| | meat | 5 (0.57) | 11 (2.70) | 20 (5.50) | 25 (8.29) | 36 (18.38) |
| 30 °C | algae | 5 (0.65) | 11 (1.67) | 19 (4.60) | 28 (8.73) | 34 (7.07) |
| | mixed | 6 (0.81) | 14 (1.94) | 27 (8.98) | 31 (10.98) | 37 (15.55) |
| | meat | 6 (0.86) | 15 (1.41) | 29 (12.40) | 50 (14.84) | 52 (13.43) |

Large differences were found in developmental stage and body size of worms reared under the different experimental conditions, indicating that both development and growth rate of *M. sanguinea* were influenced by temperature and diet.

Development seemed to be positively correlated with temperature at 15 days, whereas no effect was noted with different foods (Fig. 1). After the 45 days temperature effects were more pronounced : specimens maintained at 13 °C reached a length of 6 setigerous segments, at 18 °C growth was still slow but worms reached a length of 8 setigerous segments. At temperatures of 24, 27 and 30 °C, the specimens attained 15-19 setigers. This pattern continued to the end of the experiment. After almost 5 months the larvae reared at 13 °C still had 6 setigers (Fig. 1). In these larvae only slight changes in morphology occurred over time. The jaws became thicker, the eyes and capillary setae appeared but larvae lacked antennae, gills and new setigerous segments. At 18 °C some specimens had the central and the two median antennae. At the higher temperatures a great variability occurred within each group, whereas the difference between groups was limited (Fig. 1). At 30 °C the within-group variability was lower due to a more rapid and uniform growth. At the rearing temperature of 30 °C some specimens had five antennae and had completed larval development.

TABLE 2. — Results of two-way ANOVA testing the effects of temperature and diet on growth rate of *Marphysa sanguinea*.

| | | ANOVA | | | |
|---|---|---|---|---|---|
| Source | SS | df | MS | F ratio | P |
| T °C | 17712.737 | 6 | 2952.123 | 65.243 | 0.001 |
| diet | 16434.235 | 4 | 4108.559 | 90.801 | 0.001 |
| 2-way interaction | 786.965 | 8 | 98.371 | 2.174 | 0.001 |
| T °C diet | 786.965 | 8 | 98.371 | 2.174 | 0.001 |
| explained | 18499.702 | 14 | 1321.407 | 29.204 | 0.001 |
| residual | 34162.069 | 755 | | 45.284 | |

TABLE 3. — Results of LSD test testing the effect of temperature on growth rate of *Marphysa sanguinea* (the straight line denotes means not significantly different at 0.05 level).

| Temperature (°C) | 13 | 18 | 24 | 27 | 30 |
|---|---|---|---|---|---|
| mean length | 5.28 | 7.99 | 9.27 | 12.12 | 23.22 |

Source : MNHN, Paris

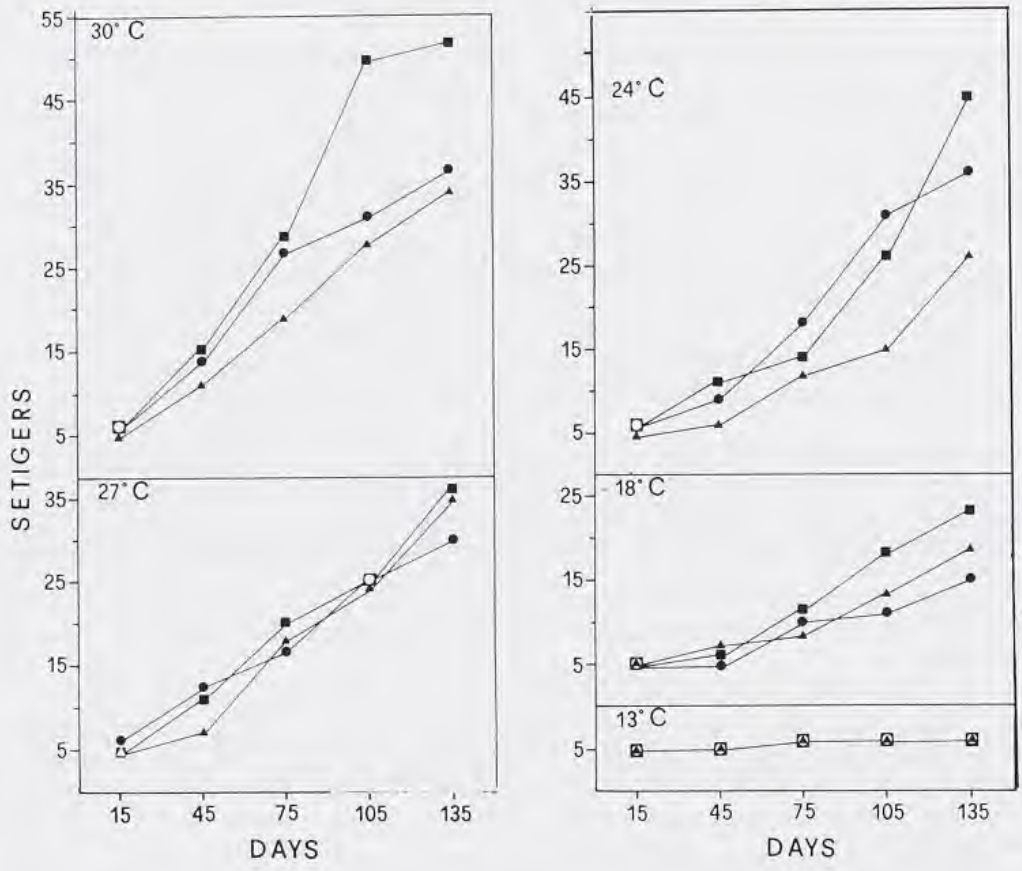



FIG. 1. — Growth rate patterns of *Marphysa sanguinea* at each treatment. (▲) algae; (●) mixed; (■) meat.

Growth rates were significantly affected by temperature and diet and a significant interaction was found between each of the two factors tested (two-way ANOVA) (Table 2). For temperature the LSD comparison of means indicated that only the means of the groups reared at 18 °C and 24 °C were not significantly different ($p > 0.05$) (Table III). For diet, the LSD test indicated that the mean growth rate observed in the groups fed with mixed or carnivorous diet were not significantly different ($p > 0.05$), whereas these were significantly different from the algae group ($p < 0.05$) (Table 4).

TABLE 4. — Results of LSD test testing effects of diet on growth rate of *Marphysa sanguinea* (the straight line denotes means not significantly different at the 0.05 level).

| Diet | algae | mixed | meat |
|---|---|---|---|
| mean length | 7.86 | 10.10 | 11.04 |

## DISCUSSION

Three conclusions can be shown from this experiment.

First, the development and growth rate of juvenile *M. sanguinea* is positively correlated with water temperature. This agrees with the findings for other species (MANGUM, 1978; WIBLE, 1984; PESCH *et al.*, 1987; BHAUD, 1988; YOKOYAMA, 1988; CHU & LEVIN, 1989; ESNAULT *et al.*, 1990 ; MIRON *et al.*, 1992; PREVEDELLI, 1992) and with observations performed in the natural environment. Indeed previous studies on the life cycle of

Source : MNHN, Paris

*M. sanguinea* found the spawning period to be from April to May, related to an increase in water temperature (PREVEDELLI, 1989). These larvae can arrest development and growth for long periods of time at lower temperature conditions. However, they maintain their potential for development under more favorable temperature conditions. If the temperature increases, the larvae will resume growth and development. This has been confirmed in laboratory studies where individuals reared at 13 °C began to grow again when placed at 18 °C. This feature is an important adaptative characteristic that permits the successful colonization of brackish waters, with variable temperatures. Seasonal fluctuations at the benthic level are stronger in lagoonal than marine environments. In particular, thermal conditions in autumn can lead to a sudden fall in temperature; in this period the larvae must be sufficiently developed to dig into sediment and reach a habitat with greater thermal stability. Temperature is an important factor regulating development and somatic growth, and its function seems especially crucial in "equilibrium" species. These species have offspring with long larval development and slow growth and must adopt strategies to reduce mortality. A strategy to maximize survival of offspring may time the reproductive period with the optimal conditions for the new generation (METTAM, 1980).

Second, the diet is a very important factor in regulating development, growth rate and survival which was lower with vegetarian diets.

Third, the findings on dietary preference demonstrate that *M. sanguinea* acquires its final omnivorous feeding habits at an early developmental stage. It is, thus, an omnivorous species, even though the vegetarian diet given did not prove to be suitable for an optimum growth.

## ACKNOWLEDGEMENTS

This paper was supported by grants from Italian MURST (Ministero dell'Università e della Ricerca scientifica e tecnologica).

## REFERENCES

BHAUD M., 1988. — Influence of temperature and food supply on development of *Eupolymnia nebulosa* (Montagu, 1818) (Polychaeta: Terebellidae). *J. exp. mar. Biol. Ecol.*, **118** : 103-113.

CHU J. W. & LEVIN L. A., 1989. — Photoperiod and temperature regulation of growth and reproduction in *Streblospio benedicti* (Polychaeta: Spionidae). *Inv. Repr. Dev.*, **15** : 131-142.

DAY J. H., 1967. — A monograph on the Polychaeta of Southern Africa. *Trust. Brit. Mus. (Nat. Hist.)*, London 878 pp.

ESNAULT G., RETIERE C. & LAMBERT R., 1990. — Food resource partitioning in a population of *Nereis diversicolor* (Annelida, Polychaeta) under experimental conditions. *In* M. BARNES & R. N. GIBSON (eds), *Trophic Relationship in the Marine Environment*, Aberdeen University Press : 453-467.

FAUCHALD K. & JUMARS P., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. Ann. Rev.*, **17** : 193-284.

GRASSLE J. F. & GRASSLE J. P., 1974. — Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. mar. Res.*, **32** : 253-284.

IVLEVA I. V., 1970. - The influence of temperature on the transformation of matter in marine invertebrates. *In*: J. H. STEELE (ed), *Marine Food Chains*. Oliver & Boyd, Edimburg : 96-112.

LEVIN L. A. & CREED E. L., 1986. — Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (Polychaeta: Spionidae) with planktotrophic or lecithotrophic development. *Mar. Biol.*, **92** : 103-113.

MANGUM C. P., 1978. — Temperature adaptation. *In* : P. J. MILL (ed), *Physiology of annelids*. Academic Press, London : 271-368.

MARSH A. G., GRÉMARE A. & TENORE K. R., 1989. — Effect of food type and ration on growth of juvenile *Capitella* sp. I (Annelida: Polychaeta): macro- and micronutrients. *Mar. Biol.*, **102** : 519-527.

MARSH A. G. & TENORE K. R., 1990. — The role of nutrition in regulating the population dynamics of opportunistic, surface deposit feeders in a mesohaline community. *Limnol. Oceanogr.*, **35** : 710-724.

Source : MNHN, Paris

McCALL P. L., 1977. — Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. mar. Res.*, **35**: 221-266.

METTAM C., 1980. — Survival strategies in estuarine nereids. In : N. V. JONES & W. J. WOLFF (eds.), *Feeding and survival strategies of estuarine organisms*. Plenum Press, New York : 65-77.

MIRON G., DESROSIERS G., RETIERE C. & MASSON S., 1992. — Variation in time budget of the polychaete *Nereis virens* as a function of density and acclimation after introduction to a new burrow. *Mar. Biol.*, **114** : 41-48.

NEUHOFF H. G., 1979. — Influence of temperature and salinity on food conversion and growth of different *Nereis* species (Polychaeta: Annelida). *Mar. Ecol. Prog. Ser.*, **1** : 255-262.

NIE N. H., HULL C. J., JENKINS J. G., STEINBRENNER K. & BENT D. H., 1975. — *SPSS : Statistical package for the social science (2nd edn)*. McGraw-Hill, New York, 675 pp.

PESCH C. E., ZAJAC R. N., WHITLATCH R. B. & BALBONI M. A., 1987. — Effect of intraspecific density on life history traits and population growth rate of *Neanthes arenaceodentata* (Polychaeta: Nereidae) in the laboratory. *Mar. Biol.*, **96** : 545-554.

PREVEDELLI D., 1989. — *Studio di una popolazione di Marphysa sanguinea (Montagu) (Polychaeta, Eunicidae) nella Laguna di Venezia : approccio autoecologico*. Doctoral Dissertation, University of Genoa.

PREVEDELLI D., 1991. — Influence of temperature and diet on survival of *Perinereis rullieri* Pilato (Polychaeta : Nereididae). *Boll. Zool.*, **58** : 225-228.

PREVEDELLI D., 1992. — Growth rates of *Perinereis rullieri* (Polychaeta, Nereididae) under different conditions of temperature and diet. *Boll. Zool.*, **59** : 261-265.

RHOADS D. C. & YOUNG D. K., 1970. — The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.*, **28** : 150-178.

TENORE K. R., 1977. — Growth of *Capitella capitata* cultured on various levels of detritus from different sources. *Limnol. Oceanogr.*, **22** : 936-941.

TENORE K. R., 1983. — Organic nitrogen and caloric content of detritus. III. Effect on growth of a deposit feedind polychaete, *Capitella capitata*. *Estuarine Coastal Shelf Sci.*, **17** : 733-742.

TENORE K. R. & CHESNEY E., 1985. — The effects of interaction of rate of food supply and population density on the bioenergetics of the opportunistic polychaete, *Capitella capitata* (type 1). *Limnol. Oceanogr.*, **30** : 1188-1195.

WIBLE J. G., 1984. — *The effects of salinity, temperature and food on the growth and reproductive output of Polydora nuchalis Woodwick (Polychaeta : Spionidae)*. Ph. D. dissertation, University of Southern California, Los Angeles, 113 pp.

WHITLATCH R. B., 1980. — Patterns of resource utilization and co-existence in marine intertidal deposit-feeding communities. *J. mar. Res.*, **38** : 743-765.

WHITLATCH R. B., 1981. — Animal - sediment relations in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. *J. exp. mar. Biol. Ecol.*, **53** : 31-45.

YOKOYAMA H., 1988. — Effects of temperature on the feeding activity and growth rate of the spionid polychaete *Paraprionospio* sp. (form A). *J. exp. mar. Biol. Ecol.*, **123** : 41-60.

ZAJAC R. N., 1986. — The effects of intra-specific density and food supply on growth and reproduction in an infaunal polychaete, *Polydora ligni* Webster. *J. mar. Res.*, **44** : 339-359.

ZAJAC R. N. & WHITLATCH R. B., 1989. — Natural and disturbance-induced demographic variation in an infaunal polychaete, *Nephtys incisa*. *Mar. Ecol. Prog. Ser.*, **57** : 89-102.

Source : MNHN, Paris

# Éthologie alimentaire d'annélides polychètes endogées : détermination du niveau sédimentaire où s'effectue la collecte de la nourriture

*Chantal SALEN-PICARD*, Claire GRAHAM** & Magali GÉRINO**

* Station Marine d'Endoume, Centre Océnologique de Marseille
URA CNRS 41, rue de la Batterie des Lions, 13007 Marseille, France
** Texas A & M University at Galveston, Department of Marine Biology
4700 Avenue U, Building 303, Galveston, USA

ABSTRACT

**Feeding ethology of infaunal polychaetous annelids: a method to determine the sediment layer at which food is collected**

Little is known about the sediment layer at which infaunal deposit feeders collect their food. A method was developped to determine the proportion of ingested sediment at a given level using a coloured marker. Individuals of the species that was investigated were placed into cores of sediment that had been previously homogenized. A layer of sediment 1 cm thick, previously mixed with fluorescent pigment of similar grain size, was placed in each core at varying depths. Animals were removed after four days and fecal pellets were collected and oven dried. Pigments were extracted and quantified using a spectrofluorimeter. Pigment concentrations in sediment and in fecal pellets allowed us to calculate the proportion of ingested sediment at a given depth. The method was used for the polychaetous annelid *Capitella capitata*. Results showed that for individuals of mean dry weight comprised between 0.75 and 1.5 mg, 54.3 ± 15.1 % of total ingested sediment was taken between 1 and 2 cm. However, some amount of sediment was ingested at deeper levels (5,4 ± 1,4 % below 3 cm deep). This, together with an inclusion of galeries and with observations in thin aquaria, suggests that *Capitella capitata* is capable of vertical movements of greater amplitude than was suspected.

RÉSUMÉ

Le niveau sédimentaire auquel s'effectue la collecte de la nourriture chez les espèces endogées dépositivores est généralement mal connu. Une méthode utilisant un traceur coloré a été mise au point afin de déterminer la proportion de sédiment ingéré à un niveau donné. Les individus de l'espèce testée sont placés dans des carottes de sédiment préalablement homogénéisé. Une couche de 1 cm d'épaisseur de sédiment mélangé à un pigment fluorescent de granulométrie semblable à celle du sédiment est intercalée dans chaque carotte à différentes profondeurs. Au bout de quatre jours les animaux sont récupérés par tamisage, leurs pelotes fécales sont récoltées et séchées à l'étuve. Le pigment est extrait et dosé à l'aide d'un spectrofluorimètre. Les concentrations du pigment dans le sédiment d'origine et dans les pelotes fécales permettent de calculer la proportion de sédiment ingéré à une profondeur donnée. La méthode testée pour l'annélide polychète *Capitella capitata* a montré que des individus d'un poids moyen compris entre 0,75 et 1,5 mg de matière sèche collectent 54,3 ± 15,1 % du sédiment total qu'ils ingèrent entre 1 et 2 cm de profondeur ; cependant une quantité non négligeable de sédiment (5,4 ± 1,4 %) est prélevée au-dessous de 3 cm. Ce résultat joint à l'observation des galeries du polychète en aquarium extra plat et d'après un moulage suggère que l'espèce est capable de déplacements verticaux d'une amplitude supérieure à ce qui est généralement admis.

---

SALEN-PICARD, C., GRAHAM, C. & M. GÉRINO, 1994. — Influence of temperature and diet on the larval development and growth of juveniles *Marphysa sanguinea* (Montagu) (Polychaeta, Eunicidae). *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 527-533. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

La quantification des flux entre les différents compartiments des systèmes marins littoraux et les tentatives d'établissement de bilans de carbone ou d'azote au sein de ces systèmes mettent souvent en évidence le manque de données relatives au rôle joué par la faune endogée (RODHOUSE & RHODEN, 1987 ; KEMP *et al.* 1990). Or, cette dernière, par sa physiologie et son éthologie représente le vecteur principal des flux et des modifications de ces flux à l'intérieur de la colonne sédimentaire et à l'interface eau-sédiment. L'influence des organismes sur les propriétés physiques et chimiques des sédiments (bioturbation) dépend, en effet, d'un certain nombre de paramètres autécologiques comme les modes d'alimentation, la profondeur d'alimentation par rapport à l'interface, le degré de mobilité, la taille des organismes, la densité de population, la profondeur des galeries et, si l'organisme est tubicole, la densité, la répartition et la longueur des tubes (RHOADS & BOYER, 1982). Indépendamment de la taille des organismes et de la densité des populations les méthodes utilisées pour déterminer ces différents paramètres sont les suivantes : 1) aquariums plats permettant l'observation directe des individus dans leurs galeries ou terriers (CLAVIER, 1984 ; DOBBS & SCHOLLY, 1986), 2) photographies et radiographies de profils sédimentaires (RHOADS & YOUNG, 1970), 3) réalisation de moulages des galeries ou terriers, technique qui permet d'appréhender leur architecture en trois dimensions (de VAUGELAS & BUSCAIL, 1990 ; GÉRINO, 1992), 4) incorporation au sédiment de traceurs radioactifs ou colorés afin de déterminer le sens et l'intensité des échanges entre l'interface eau-sédiment et les différents niveaux de la colonne sédimentaire (MAHAUT & GRAF, 1987 ; GÉRINO, 1990) ou bien le taux d'ingestion pour les espèces dépositivores de surface (CAMMEN, 1980a). Les espèces de l'endofaune sont, pour beaucoup d'entre elles, dépositivores et ces différentes méthodes, exception faite pour les espèces qui s'alimentent à l'interface eau-sédiment ou pour celles qui construisent des terriers permanents, ne permettent pas de déterminer la profondeur à laquelle elles collectent leur nourriture.

Dans le but d'intégrer la faune endogée dans les bilans de nutriments d'une baie des parages de Marseille occupée par un élevage de *Mytilus galloprovincialis* (anse de Carteau, golfe de Fos), nous avons été amenés à acquérir des informations sur l'éthologie alimentaire de l'annélide polychète *Capitella capitata* présent en densité élevée (jusqu'à 400 000 ind. $m^{-2}$) dans le sédiment sous jacent aux cultures de moules (BAUDINET *et al.*, 1990). Nous avons, pour cela, mis au point une méthode expérimentale utilisant un traceur coloré permettant non seulement de visualiser le niveau sédimentaire auquel l'espèce collecte sa nourriture mais aussi de déterminer la proportion de sédiment ingéré à un niveau donné. L'observation des galeries en aquarium extra plat (1 mm d'épaisseur) et la réalisation d'un moulage ont permis de compléter nos observations sur le comportement de l'espèce.

## MATÉRIEL ET MÉTHODES

### 1) UTILISATION D'UN TRACEUR COLORÉ.

Principe de la méthode. — Le but du travail était de mettre au point une méthode permettant de déterminer le niveau sédimentaire auquel les espèces de l'endofaune collectent préférentiellement leur nourriture. Des individus de l'espèce test (*Capitella capitata*) ont été introduits dans des carottes de sédiment reconstituées comportant à une profondeur donnée une couche de sédiment coloré. Le substrat coloré a été obtenu en mélangeant au sédiment un pigment fluorescent. Le dosage, par une méthode optique, du pigment contenu dans les pelotes fécales des animaux devait permettre d'évaluer la proportion de sédiment ingéré à une profondeur donnée.

L'espèce testée *C. capitata* provient des biodépôts issus de l'élevage de *Mytilus galloprovincialis*. Le ou les types de *C. capitata* présents sous les cultures de moules n'ont pas été déterminés. Tous les individus utilisés au cours des différentes expériences sont cependant issus d'un même couple et proviennent d'un élevage réalisé au laboratoire à température et à salinité constantes (17 °C et 33 P.S.U.).

Le sédiment utilisé a été récolté sous les cultures de moules par 5 m de profondeur ; seule la partie superficielle du substrat (0-2 cm) a été prélevée, tamisée sur une maille de 0,5 mm, homogénéisée puis congelée afin d'en éliminer la faune vivante. Le pigment employé pour colorer le sédiment est un pigment fluorescent servant de base pour des peintures industrielles, pulvérulent, non soluble dans l'eau mais soluble dans l'acétone et d'une granulométrie voisine de celle du sédiment utilisé (plus de 90 % d'éléments d'un diamètre ≤ 0,063 mm). Après addition du pigment le sédiment a été à nouveau homogénéisé.

Protocole expérimental. — Des carottiers en plexiglas d'un diamètre intérieur de 7,5 cm ont été remplis d'une couche de sédiment de 8 cm d'épaisseur à raison d'un carottier témoin sans colorant, de quatre carottiers ayant respectivement une couche colorée de 0 à 1 cm, de 1 à 2 cm, de 2 à 3 cm et de 3 à 8 cm et d'un carottier ne contenant que du sédiment coloré. Au fur et à mesure du remplissage des carottiers, des échantillons de sédiment ont été prélevés aux différents niveaux ; après lyophilisation, leurs teneurs en azote et carbone ont été déterminées (CHN analyser LECO) ; la fraction organique a été obtenue par différence entre teneur en carbone total et teneur en carbone après combustion à 450 °C (KRISTENSEN & ANDERSEN, 1987) ; les résultats ont été exprimés en pourcentage du poids de matière sèche.

Source : MNHN, Paris

Vingt individus de *C. capitata* de taille moyenne (environ 1 mg de matière sèche) ont été introduits dans chaque carottier ; trois replicats ont été réalisés. Le système a été maintenu pendant 4 jours à 17°C dans un courant continu d'eau de mer aérée ; aucun apport de nourriture n'a été effectué pendant cette période.

En fin d'expérience, les animaux ont été récupérés par tamisage sur une maille de 0,3 mm ; tous les animaux n'ayant pas été récupérés (mortalité, fuite), on n'a conservé pour chaque carottier qu'un nombre d'individus correspondant au nombre minimum récupéré soit 10 individus. Les vers ont été transférés dans de l'eau de mer filtrée sur 0,2 µm et laissés pendant 12 h. Les pelotes fécales émises pendant ce laps de temps ont été au fur et à mesure prélevées à la micropipette, rincées à l'eau distillée afin d'en éliminer l'excès de sel, récoltées sur filtres GF/C prépesés (toutes les pelotes provenant des 10 individus conservés pour un même carottier ont été regroupées) puis séchées à l'étuve à 40 °C pendant 12 h. Le poids de matière sèche des fèces a ensuite été exprimé à 10 µg près.

L'extraction du pigment dans de l'acétone à 90 % et son dosage ont été réalisés selon le même procédé que celui utilisé pour le dosage des pigments chlorophylliens (AMINOT & CHAUSSEPIED, 1983). Les densités optiques ont été lues sur spectrofluorimètre Kontron SFM/B ; outre une puissance de dosage élevée, le spectrofluorimètre a permis de déterminer les longueurs d'onde d'excitation maximum (464 nm) et d'émission (493 nm) du pigment utilisé. La réalisation d'une gamme étalon à partir de concentrations connues du pigment a permis de déterminer, pour chaque échantillon, la concentration du pigment dans l'acétone (en mg. $ml^{-1}$) puis dans les fèces (en ng. $mg^{-1}$ de matière sèche). De la même façon, la concentration moyenne en pigment du sédiment d'origine a été déterminée. Le pourcentage de sédiment coloré ingéré par rapport au sédiment total ingéré est donné par la formule :

$$Pi = \frac{Cf \times 100}{Cs}$$

où : Pi = pourcentage de sédiment coloré ingéré
Cf = Concentration du pigment dans les fèces
Cs = Concentration du pigment dans le sédiment coloré utilisé.

On a testé statistiquement (ANOVA et test t) 1) l'influence du pigment sur la quantité de sédiment ingéré, sur le taux de survie et sur la richesse en carbone et en azote du sédiment ; 2) la non assimilation et l'absence de sélection du pigment : on a déterminé si la concentration du pigment dans les fèces des animaux ayant séjourné dans les carottiers remplis uniquement de sédiment coloré est comparable à la concentration du pigment dans le sédiment ; 3) si la quantité de sédiment coloré ingéré est significativement différente en fonction de la profondeur. L'intervalle de confiance sur toutes les moyennes qui ont été calculées est exprimé avec un coefficient de sécurité de 95 %.

2) OBSERVATION DES GALERIES.

L'observation des galeries a été effectuée grace à la réalisation de deux aquariums extra plats démontables pour en faciliter le remplissage et d'un moulage. Le moulage a été exécuté selon la technique de PERVESLER & DWORSCHAK (1985) adaptée par GÉRINO & STORA (1991). Le résultat obtenu correspond aux galeries réalisées par cinq individus de taille moyenne après quatre semaines de conditions in vitro dans un carottier analogue à ceux déjà utilisés.

## RÉSULTATS

1. GAMME ÉTALON DU PIGMENT ET CONCENTRATION DANS LE SÉDIMENT COLORÉ.

La gamme étalon réalisée à partir de six concentrations connues du pigment a permis d'établir l'équation de la droite de régression de la concentration du pigment dans l'acétone en fonction de la densité optique :

$C = 0{,}00027.DO + 0{,}0012$, où C = concentration du pigment dans l'acétone en $mg.ml^{-1}$ ; DO = Densité optique ; $r = 0{,}995$ ** ($P \geq 99$ %).

La concentration moyenne en pigment du mélange sédiment + colorant est de $0{,}0765 \pm 0{,}043$ g par g de sédiment sec.

2. INFLUENCE DU PIGMENT SUR LA RICHESSE EN CARBONE ET EN AZOTE DU SÉDIMENT.

L'ANOVA réalisée d'après l'analyse des différents échantillons a montré que l'addition de pigment augmente de façon significative les teneurs en carbone et en azote mais que l'homogénéisation a été suffisante pour qu'il n'y ait pas de différence entre les couches colorées des divers carottiers. Le tableau 1 donne les teneurs moyennes en azote et en carbone total du sédiment et du mélange sédiment + colorant en fonction de la profondeur. La teneur en carbone organique égale à environ 50 % du carbone total dans le sédiment d'origine atteint 70 % dans le mélange sédiment + colorant.

Source : MNHN, Paris

TABLEAU 1. — Teneurs moyennes en carbone total et en azote dans le sédiment et dans le mélange sédiment + colorant en fonction de la profondeur.

| | Sédiment | | Sédiment + colorant | |
|---|---|---|---|---|
| | % C total | % N | % C total | % N |
| 0 - 1 cm | 5,76 ± 1,40 | 0,30 ± 0,08 | 9,14 ± 1,21 | 2,30 ± 1,22 |
| 1 - 2 cm | 5,86 ± 0,12 | 0,25 ± 0,03 | 8,21 ± 2,25 | 2,00 ± 0,51 |
| 2 - 3 cm | 5,95 ± 0,62 | 0,25 ± 0,04 | 9,39 ± 0,71 | 1,98 ± 0,88 |
| > 3 cm | 5,55 ± 0,36 | 0,27 ± 0,07 | 9,20 ± 1,23 | 2,16 ± 0,61 |

3. INFLUENCE DU PIGMENT SUR LA QUANTITE DE FÈCES ÉMISES ET SUR LE NOMBRE DE SURVIVANTS.

Le poids moyen individuel de fèces émises est de 1,37 ± 0,25 mg de matière sèche. Il n'y a pas de différence significative entre les divers traitements ; on ne peut pas conclure à une influence du colorant sur la quantité de pelotes fécales émises.

Le nombre d'individus survivants varie de 10 à 19. La différence entre les différents carottiers n'est pas significative. Le nombre moyen d'individus survivants pour l'ensemble des traitements est de 12 ± 2 individus.

4. TEST DE NON ASSIMILATION ET D'ABSENCE DE SÉLECTION DU PIGMENT.

Le test t effectué entre la moyenne (0,0765 ± 0,043 g. $g^{-1}$ de sédiment sec) des concentrations du pigment dans le sédiment coloré et la moyenne (0,0688 ± 0,027 g. $g^{-1}$ de matière sèche) des concentrations du pigment dans les pelotes fécales des individus ayant séjourné dans les carottiers remplis en totalité de sédiment coloré ne permet pas de conclure avec un coefficient de sécurité suffisant ($P \leq 60$ %) à une différence entre les deux concentrations.

5) PROPORTION DE SÉDIMENT COLORÉ INGÉRÉ EN FONCTION DE LA PROFONDEUR DE LA COUCHE COLORÉE.

La figure 1 donne, pour chaque profondeur, la proportion moyenne de sédiment coloré ingéré par *C. capitata*. Le maximum de sédiment coloré a été ingéré (54,3 ± 15,1 %) lorsque la couche colorée est située entre 1 et 2 cm. La différence entre les divers niveaux est hautement significative. De plus, l'écart entre les concentrations du pigment dans les fèces aux différentes profondeurs est statistiquement supérieur à l'hétérogénéité des concentrations dans le sédiment coloré utilisé.

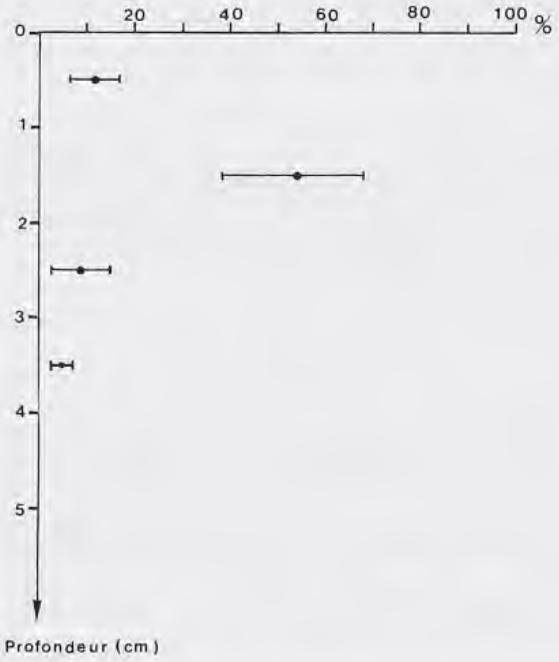



FIG. 1. — Pourcentage de sédiment ingéré par *Capitella capitata* en fonction de la profondeur.

6) OBSERVATIONS DES GALERIES.

Dans les deux cas (aquariums extra plats et moulage) on a observé une forte concentration de galeries dans les deux premiers cm du sédiment (Fig. 2) ; cependant on remarque la présence de galeries descendant jusqu'à plus de 10 cm de profondeur. Les galeries présentent de nombreuses bifurcations et plusieurs orifices de communication avec l'interface eau-sédiment, orifices par où sont évacuées les pelotes fécales.

Source : MNHN, Paris

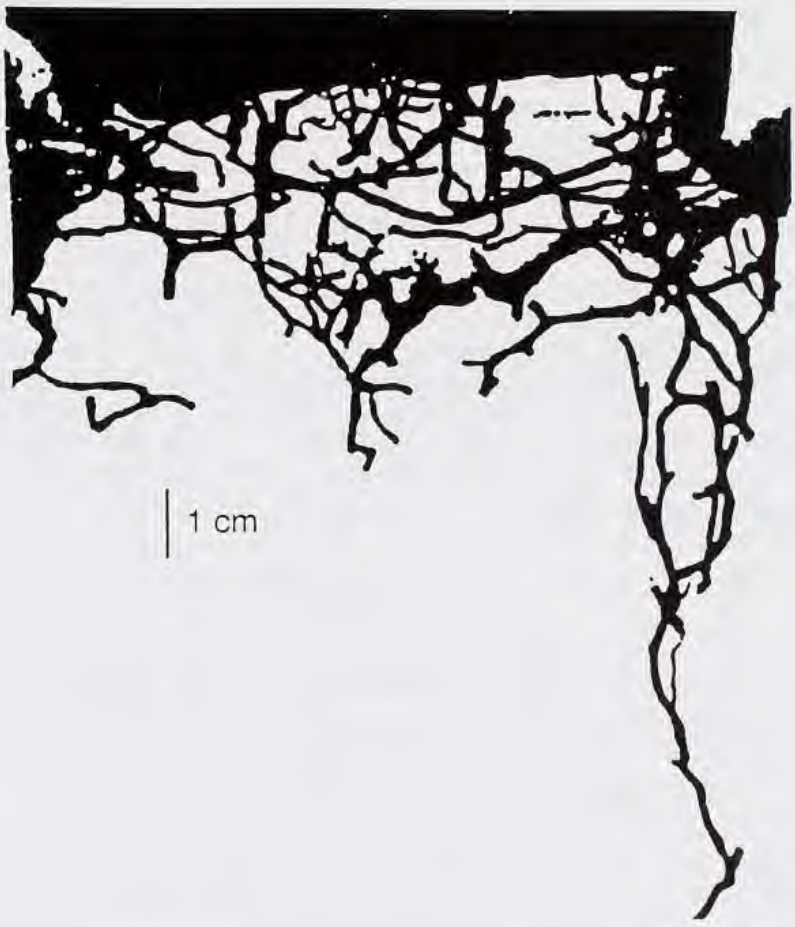



FIG. 2. — Moulage des galeries construites par cinq individus de *Capitella capitata* après quatre semaines de conditions *in vitro*.

## DISCUSSION CONCLUSION

La méthode a montré de façon significative que les individus testés ont un niveau préférentiel de collecte de leur nourriture. Dans les études consacrées à l'éthologie alimentaire des espèces dépositivores, les traceurs colorés n'avaient guère été utilisés qu'en tant que marqueurs qualitatifs (HAVEN & MORALES-ALAMO, 1966 ; JACOBSEN, 1967 ; CAMMEN, 1980 a, b ; DOBBS & WHITLATCH, 1982). Le fait d'utiliser un pigment fluorescent soluble dans l'acétone a permis son extraction et sa quantification. La comparaison avec le témoin sans colorant a montré que le pigment n'est pas, tout au moins à court terme, toxique pour les animaux et qu'il ne modifie pas la quantité de pelotes fécales émises. Pour que le rapport concentration du pigment dans les fèces/concentration du pigment dans le sédiment ingéré soit représentatif de la proportion de sédiment coloré ingéré, il faut 1) que le pigment ne soit pas assimilable, 2) que l'espèce testée ne soit pas trop sélective dans la collecte de sa nourriture ; toutes conditions qui ont été réunies dans le cas présent. Plutôt que d'utiliser un sédiment ayant conservé sa stratification naturelle, nous avons préféré employer un sédiment homogénéisé afin d'éliminer l'influence de la richesse du substrat. L'addition du pigment enrichit cependant le sédiment en azote total et en carbone organique mais l'homogénéisation du mélange sédiment + colorant a été suffisante pour que l'enrichissement soit équivalent quel que soit le niveau coloré considéré. Les résultats obtenus sont indépendants de la richesse du substrat et traduisent bien un comportement de l'espèce.

De nombreux travaux récents menés par TENORE et ses collaborateurs (MARSH *et al.*, 1989) ont été consacrés au rôle joué par la quantité et par la qualité de l'alimentation sur la croissance individuelle et la dynamique de population de *C. capitata* type I. Le taux d'égestion et la variabilité de ce dernier en fonction de contraintes physicochimiques (température, oxygène) ou individuelles (croissance) ont été étudiés par FORBES & LOPEZ (1990) mais l'éthologie et l'influence des espèces du genre *Capitella* sur le sédiment restent mal connues. Contrairement aux grands terriers permanents construits par des espèces qui ont d'importantes capacités de bioturbation, les

Source : MNHN, Paris

structures biogènes produites par les espèces pionnières ont reçu peu d'attention (ALONGI, 1985). D'après FAUCHALD & JUMARS (1979) *Capitella* construit des tubes muqueux près de la surface du sédiment ; RHOADS & BOYER (1982) considérant que les espèces pionnières s'alimentent à ou au dessus de l'interface eau-sédiment stipulent que leur influence sur le substrat est limitée à une épaisseur inférieure à 2 cm. Notre méthode a clairement démontré que *C. capitata* est une espèce dépositivore de subsurface, la zone d'ingestion maximale pour des individus de taille moyenne se trouvant localisée entre 1 et 2 cm de profondeur. Une quantité encore importante de sédiment est ingérée au dessous de 3 cm ; ce résultat associé aux observations réalisées en aquariums extra plats et au moulage des galeries confirme le fait que l'espèce est capable de mouvements verticaux d'une amplitude supérieure à ce qui est généralement admis. L'étude du peuplement de *Capitella capitata* installé sous les cultures de moules a révélé une stratification des individus en fonction de leur taille et de leur âge : les individus juvéniles et de petite taille sont localisés entre 0 et 1 cm, ceux de grande taille (poids ≥ 1,5 mg) ont un maximum d'abondance entre 4 et 6 cm de profondeur. La méthode appliquée aux différentes classes de taille d'une population, devrait donc permettre de déterminer la zone d'ingestion maximale à l'échelle de la population ; de là, connaissant la distribution verticale dans le sédiment d'un certain nombre de macro et de micronutriments, il sera possible de mieux appréhender les besoins de l'espèce et l'évolution de ces besoins en fonction de l'âge des individus. De plus, chez les espèces dépositivores de subsurface qui évacuent leurs pelotes fécales à la surface du sédiment, le fait de connaître la proportion de sédiment ingéré à une profondeur donnée peut rendre plus aisée la détermination des taux de remaniement sédimentaire en limitant la récolte des pelotes fécales aux seuls éléments colorés ou après utilisation de techniques de traitement d'images.

## REMERCIEMENTS

Ce travail a été exécuté, pour l'une d'entre nous, dans le cadre du programme de bourses ERASMUS ; il a bénéficié du soutien du Groupement Scientifique CNRS Université d'Aix Marseille II. Société Nationale Elf Aquitaine : Cycles biogéochimiques. Devenir de la matière organique dans le milieu littoral marin.

## RÉFÉRENCES

ALONGI, D.M., 1985. — Microbes, meiofauna and bacterial productivity on tubes constructed by the polychaete *Capitella capitata*. *Mar. Ecol. Progr. Ser.*, **23** : 207-208.

AMINOT, A. & CHAUSSEPIED, M., 1983. — *Manuel des analyses chimiques en milieu marin*. C.N.E.X.O. Publ., Brest, 395 pp.

BAUDINET, D., ALLIOT, E., BERLAND, B., GRENZ, C., PLANTE CUNY, M.R., PLANTE, R. & SALEN PICARD, C., 1990. — Incidence of mussel culture on biogeochemical fluxes at the sediment water interface. *Hydrobiologia*, **207** : 187-196.

CAMMEN, L.M., 1980a. — A method for mesuring ingestion rate of deposit feeders and its use with the polychaete *Nereis succinea*. *Estuaries*, **3** : 55-60.

CAMMEN, L.M., 1980b. — The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. *Mar. Biol.*, **61** : 9-20.

CLAVIER, J., 1984. — Production due to regeneration by *Euclymene oerstedi* (Claparède) (Polychaeta: Maldanidae) in the maritim Basin of the Rance (Northern Britany). *J. exp. mar. Biol. Ecol.*, **75** : 97-106.

DOBBS, F.C. & SCHOLLY, T.A., 1986. - Sediment processing and selective feeding by *Pectinaria koreni* (Polychaeta: Pectinariidae). *Mar. Ecol. progr. Ser.*, **29** : 165-176.

DOBBS, F.C. & WHITLATCH, R.B., 1982. — Aspects of deposit feeding by the polychaete *Clymenella torquata*. *Ophelia*, **21** : 159-166.

FAUCHALD, K. & JUMARS, P.A., 1979. — The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. Ann. Rev.*, **17** : 193-284.

FORBES, T.L. & LOPEZ, G.R., 1990. — Ontogenic changes in individual growth and egestion rates in the deposit feeding polychaete *Capitella* sp. I. *J. exp. mar. Biol. Ecol.*, **143** : 209-220.

GÉRINO, M., 1990. - The effects of bioturbation on particle redistribution in Mediterranean coastal sediment. Preliminary results. *Hydrobiologia*, **207** : 251-258.

GÉRINO, M., 1992. — *Étude expérimentale de la bioturbation en milieux littoral et profond. Quantification des structures de bioturbation et modélisation du remaniement biologique du sédiment*. Thèse Doct. Univ. Aix Marseille II, 207 pp.

GÉRINO, M. & STORA, G., 1991. — Analyse quantitative de la bioturbation induite par la polychète *Nereis diversicolor*. *C. R. Acad. Sci.*, Paris, **313** : 489-494.

Source : MNHN, Paris

HAVEN, D.S. & MORALES ALAMO, R., 1966. — Use of fluorescent particles to trace oyster biodeposits in marine sediments. *J. Cons. perm. Int. Explor. Mer*, **30** : 267-269.

JACOBSEN, V.H., 1967. — The feeding of the lugworm *Arenicola marina* (L.). Quantitative studies. *Ophelia*, **4** : 91-109.

KEMP, W.M., SAMPOU, P., CAFFREY, J., MAYER, M., HENRIKSEN, K. & BOYNTON, W.R., 1990. — Ammonium recycling versus denitrification in Chesapeake Bay sediments. *Limnol. Oceanogr.*, **35** : 1545-1563.

KRISTENSEN, E. & ANDERSEN, F.O., 1987. — Determination of organic carbon in marine sediments ; a comparison of two CHN analyzer methods. *J. exp. mar. Biol. Ecol.*, **109** : 15-23.

MAHAUT, M.L.& GRAF, G., 1987. — A luminophore tracer technique for bioturbation studies. *Oceanol. Acta*, **10** : 323-328.

MARSH, A.G., GREMARE, A. & TENORE, K.R., 1989. — Effect of food type and ration on growth of juvenile *Capitella* sp. I (Annelida: Polychaeta): macro and micronutrients. *Mar. Biol.*, **102** : 519-527.

PERVESLER, P. & DWORSCHAK, P.C., 1985. — Burrows of *Jaxea nocturna* Nardo in the gulf of Trieste. *Senckenbergiana marit.*, **17** : 33-53.

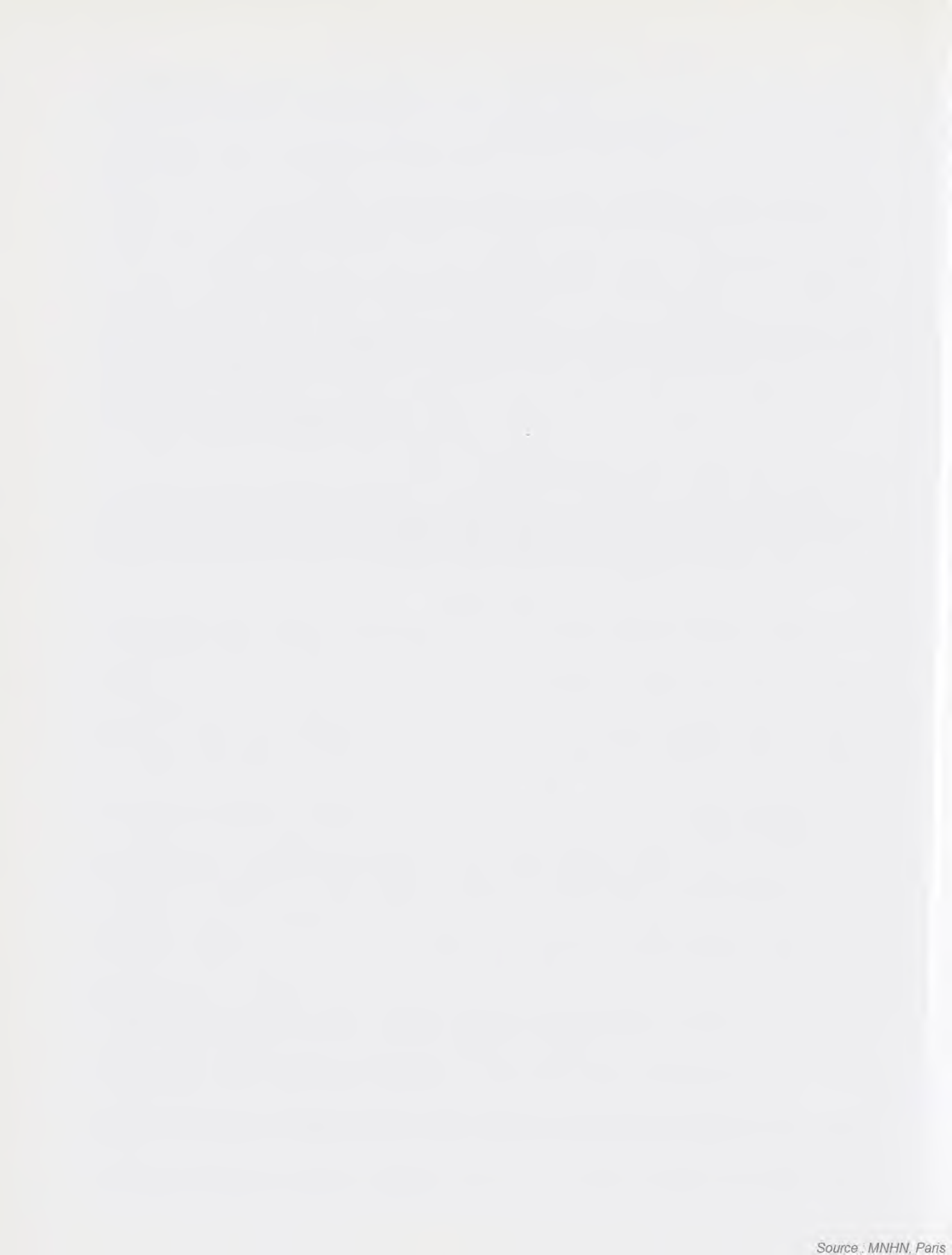
RHOADS, D.C. & BOYER, L.F., 1982. — The effects of marine benthos on physical properties of sediments. A successional perspective. *In*: P.L. Mc CALL & M.J.S. TEVESZ (eds), *Animal sediment relations*. Plenum N.Y. : 3-52.

RHOADS, D.C. & YOUNG, D.K., 1970. — The influence of deposit feeding organisms on sediment stability and community trophic structure. *J. mar. Res.*, **28** : 150-178.

RODHOUSE, P.G. & RODEN, C.M., 1987. — Carbon budget for a coastal inlet in relation to intensive cultivation of suspension feeding bivalve molluscs. *Mar. Ecol. Progr. Ser.*, **36** : 225-236.

VAUGELAS, J. de & BUSCAIL, R., 1990. — Organic matter distribution in burrows of the thalassinid crustacean *Callichirus laurae*, Gulf of Aquaba (Red Sea). *Hydrobiologia*, **207** : 269-277.

Source : MNHN, Paris



Source : MNHN, Paris

# Polychaete distribution patterns on *Chlamys patagonica* of the Magellan Strait

*Rossana SANFILIPPO*

Istituto Policattedra di Oceanologia e Paleoecologia
Corso Italia, 55
95129 Catania, Italy

ABSTRACT

The composition of the community with epibiont polychaetes on a population of *Chlamys patagonica* (King & Bodrerip) was studied together with the rates of covering on the opposite valves and the distribution patterns. A clear differentiation was noted between the covering of the right valves and the left ones, which on average, for the polychaetes is 0.7 % an the right valves but 4.2 % on the left ones. Differences were noted in the patterns and rates of colonization of some polychaete species. *Serpula narconensis* and the sabellariid *Idanthyrsus armatus* were rare on small *Chlamys*, but very common on medium and large ones, averaging about 9 % cover on the left (uppermost) valve in large *Chlamys*, but less than 1 % on the right valve. They ranked fourth, behind bryozoans, sponges and algae, in their contribution to a rich epizoan community, which covered about half the surfaces of both valves, even in small *Chlamys*, and became denser with age. In contrast the spirorbid *Protolaeospira lebruni* was much more numerous on right than left valves, and on small than large *Chlamys*, suggesting that initial colonisation by spirorbids may occur during the juvenile stage, when the *Chlamys* are attached to rocks.

RÉSUMÉ

**Modalités de distribution de Polychètes sur *Chlamys patagonica* du détroit de Magellan**

La composition d'un peuplement de polychètes épibiontes sur une population de *Chlamys patagonica* et ses rapports avec les autres organismes sessiles ont été étudiées. On a examiné les taux de recouvrement sur les valves opposées ainsi que les modalités de distribution des épibiontes. Une nette différenciation de ces recouvrements a été observée : ils ont (pour les polychètes) des valeurs moyennes de 0,7 % sur les valves de droite et de 4,2 % sur les valves de gauche. Le recouvrement total croît rapidement avec la taille des *Chlamys*. De profondes différences ont également été relevées dans les modalités et le temps de colonisation chez quelques espèces de polychètes. *Serpula narconensis* et le sabellariide *Idanthyrsus armatus* suivent la tendance générale d'augmentation du recouvrement au cours de la croissance des *Chlamys*, atteignant un recouvrement d'environ 9 % sur les valves de gauche des *Chlamys* les plus âgés, mais seulement 1 % sur les valves de droite. Ces espèces participent, en quatrième position, après les bryozoaires, les éponges et les algues, à la formation d'une riche communauté d'épizoaires laquelle recouvre environ la moitié de la surface des deux valves, même chez les jeunes *Chlamys*, et qui devient plus dense avec l'âge. Au contraire, le spirorbe *Protolaeospira lebruni* présente une colonisation initiale rapide des deux valves des *Chlamys* de petite taille, ce qui suggère que cette colonisation initiale des spirorbes peut avoir lieu durant la période juvénile des *Chlamys*, lorsqu'ils sont encore attachés aux rochers.

---

SANFILIPPO, R., 1994. — Polychaete distribution patterns on *Chlamys patagonica* of the Magellan Strait. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 535-540. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

As part of an Italian research program on subantarctic areas, an oceanographic expedition visited the Magellan Strait in February-March 1991. The station examined was rich in the pectinid bivalve *Chlamys patagonica* (King & Broderip). Specimens measured up to 8 cm in length and were densely covered with epibionts. This scallop is commercially important and is fished along the Argentinian shelf. Adults belong to the vagile epifauna whereas juveniles attach to the substratum by means of the byssus, but these juveniles were rare in the population examined. This is probably because juveniles do not live in the same area as the adults as in other pectinids (WALOSZEK & WALOSZEK, 1986; DI GERONIMO & ROSSO, 1990). When at rest, adults lie on the substratum on the right valve, which is white and slightly convex, whereas the left valve is turned up, brownish red and more convex. Swimming occurs briefly and rather rarely. *Chlamys patagonica* lives on soft bottoms that can be characterized as sandy to gravelly-sandy. Its shells are among the larger available substrata for attachment of sessile epifauna.

## MATERIAL

The study is based on 50 specimens of *C. patagonica* obtained alive at station 21, 52°52,7' S, 70°31,8' W, at a depth of 80 m, North-East of Punta Arenas, in the southernmost part of Paso Ancho, near the mouth of the Segunda Angostura (Fig. 1).

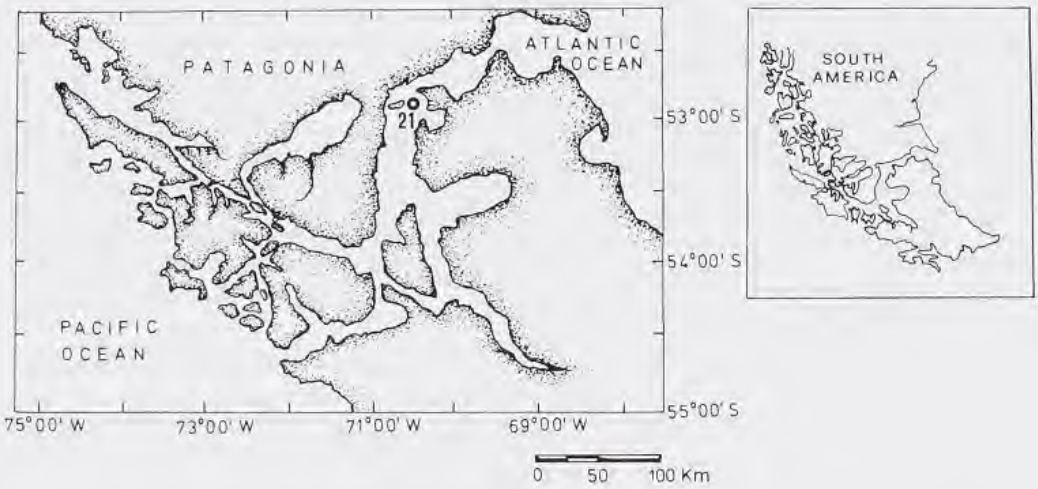



FIG. 1. — Location of station 21

The area is characterized by a sustained hydrodynamism and by turbulent and irregular currents (BRAMBATI *et al.*, 1991). The substratum is gravelly sand with no muddy fraction. *Chlamys patagonica* is both alive and dead (disarticulated valves). Large pebbles and the scallop shells are densely colonized by numerous epibionts. The station is also characterized by the abundance of sponges, gasteropods (trochids), decapod crustaceans, echinoids, asteroids, ophiuroids and ascidians. Mollusk shells dominate the thanatocoenosis (DI GERONIMO *et al.*, 1992).

## METHODS

The percentage of the surface occupied by polychaete tubes was calculated for each valve with respect to the total area. The sample of *Chlamys* was then subdivided into three size classes each corresponding to a different growth stage (Table 1). The growth rate of *C. patagonica* is slow; according to WALOSZEK & WALOSZEK (1986),

Source : MNHN, Paris

this species needs 3-5 years to reach a size of 50-60 mm. The average dominance value of each polychaete species is given for each size group, the composition of the epifauna varying with the age (i.e. size) of the single pectinid. The patterns of encrusting species found on each shell (left and right valves) were drawn, showing the position and relative areas covered by each of the polychaete species. The shells mapped were arbitrarily divided into nine regions and the percentage cover of each species was estimated for each region and was then calculated for the three size classes, roughly following the method used by WARD & THORPE (1991).

TABLE 1. — Subdivision into three size classes of the sample of *Chlamys patagonica*.

| | Length (mm) | Width (mm) | Thickness (mm) |
|---|---|---|---|
| Group A | < 3.5 | < 3.5 | < 1.4 |
| Group B | 3.5 - 6.2 | 3.5 - 6.1 | 1.4 - 1.2 |
| Group C | > 6.3 | > 6.2 | > 2.1 |

The area is characterized by a sustained hydrodynamism and by turbulent and irregular currents (BRAMBATI *et al.*, 1991). The substratum is gravelly sand with no muddy fraction. *Chlamys patagonica* is both alive and dead (disarticulated valves). Large pebbles and the scallop shells are densely colonized by numerous epibionts. The station is also characterized by the abundance of sponges, gasteropods (trochids), decapod crustaceans, echinoids, asteroids, ophiuroids and ascidians. Mollusk shells dominate the thanatocoenosis (DI GERONIMO *et al.*, 1992).

## RESULTS

The data collected provided information on the composition of the epifauna and distribution of the polychaete species and other epibionts. Epibionts (ROSSO & SANFILIPPO, 1992) essentially belong to a few group of organisms (Table 2).

TABLE 2. — Epibiont groups on *Chlamys patagonica*.

| Epizoan community on *Chlamys patagonica* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Group A | | Group B | | Group C | | TOTAL | |
| | Left | Right | Left | Right | Left | Right | Left | Right |
| | % | % | % | % | % | % | % | % |
| Bryozoans | 27.7 | 8.0 | 35.0 | 25.8 | 48.3 | 40.6 | 36.5 | 25.0 |
| Sponges | 32.1 | 3.0 | 18.3 | 21.4 | 13.6 | 6.8 | 20.6 | 13.4 |
| Algae | | 34.1 | 4.2 | 3.8 | 0.4 | 3.1 | 2.2 | 11.2 |
| Polychaetes | | 1.0 | 2.7 | 0.7 | 9.7 | 0.7 | 4.2 | 0.7 |
| Hydroids | | | 0.6 | 0.4 | 3.2 | 2.7 | 1.1 | 0.9 |
| Barnacles | | | | | 0.5 | | 0.1 | |
| Brachiopods | | | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| Bivalves | | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| Foraminifers | | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| Others | | | 0.1 | | 1 | 0.1 | 0.3 | 0.1 |
| **TOTAL COVERING** | **59.8** | **46.3** | **61.2** | **52.4** | **77.0** | **54.3** | **65.3** | **51.6** |

Bryozoans and sponges are dominant, followed by the green algae; whereas, polychaetes and hydroids are subordinate. The composition of the epifauna differed between the right and left valves. The left valves are colonized by epibionts which develop in height like large agglutinant polychaetes, colonies of celleporiform bryozoans, large barnacles, brachiopods and erect hydroids. On the contrary, the right valves are dominated by less voluminous forms like membraniporiform bryozoans and spirorbids. The differentiation between the opposite

Source : MNHN, Paris

valves is also shown by the average total covering: 51.6 % on the right valves, 65.3% on the left valves. On some valves the covering may even reach and exceed 100 %. The total covering tends to increase from the smaller sized scallops to the larger ones, a phenomenon particularly evident in bryozoans and hydroids.

Five species of polychaetes were identified including three Spirorbidae, one Serpulidae and one Sabellariidae (Table 3). Four were common and widespread around the southern part of South America and Magellan strait (HARTMAN, 1966; KNIGHT-JONES & KNIGHT-JONES, 1984, 1991), whereas *Romanchella* cf. *inventis* was here recorded for the first time. Instead *R. inventis* was only known from the subantarctic Tristan da Cunha and Marion Islands (HARRIS, 1969; KNIGHT-JONES & KNIGHT-JONES, 1984).

Tubes of *Serpula narconensis* from Magellan station 21 and other subantarctic areas have a pink or light orange colouring, whereas tubes from high latitude Antarctica were entirely white and opaque. In fact, the Magellan Strait tubes have a thin, coloured, transparent outer layer. It was also observed that juvenile tubes were morphologically different: they were devoid of the pigmented transparent outer layer and appeared white, with three longitudinal, toothed keels. The keels disappear in the adults and the tube tends to become smooth, in contrast to young specimens.

TABLE 3. — List of polychaete species identified on *Chlamys patagonica*.

| Polychaete community on *Chlamys patagonica* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| POLYCHAETA | Group A | | Group B | | Group C | | TOTAL | |
| | Left | Right | Left | Right | Left | Right | Left | Right |
| | % | % | % | % | % | % | % | % |
| SABELLARIIDAE | | | | | | | | |
| *Idanthyrsus armatus* Kinberg | | | 1.9 | | 8.6 | | 3.5 | |
| SERPULIDAE | | | | | | | | |
| Serpula narconensis Baird | | | 0.4 | 0.2 | 0.6 | 0.2 | 0.3 | 0.1 |
| Serpulidae spp. | | | | 0.1 | | | | |
| SPIRORBIDAE | | | | | | | | |
| *Protolaeospira lebruni* (Caullery & Mesnil) | | 0.6 | 0.2 | 0.2 | 0.1 | 0.4 | 0.1 | 0.4 |
| *Romanchella perrieri* (var.a) Caullery & Mesnil) | | | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| *Romanchella* cf. *inventis* (Harris) | | | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| Spirorbidae spp. | | | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| Others | | | 0.1 | 0.3 | 0.4 | 0.1 | 0.1 | 0.1 |
| **TOTAL COVERING** | **0.0** | **0.6** | **3.0** | **1.1** | **10.0** | **1.0** | **4.3** | **0.9** |

The average total surface covering by these species showed a higher rate of encrustation on the left valves (4.2 %) than on the right (0.7 %). Similarly, the total covering increased as the pectinids grew larger. Although the serpulids and sabellariids were more common in larger scallops, the reverse was true for the spirorbids (Fig. 2).

*S. narconensis* was not present on the smallest pectinids (group A) and colonized only medium to large scallops which thereby followed the general trend of the other epibionts (Fig. 2). The average covering by *S. narconensis* was higher on the left valves (0.4 % and 0.6 % of groups B and C) compared to the right ones (0.2 % and 0.2 % of groups B and C).

The sabellariid *Idanthyrsus armatus* showed, even more markedly, the same distribution trend as *S. narconensis*: its big agglutinant tubes encrust only the left valves of medium and large sized scallops, with covering values from 1.9 % to 8.6 %.

The spirorbid *Protolaeospira lebruni* colonizes all three size groups. More right valves are covered than left ones which is the reverse of that observed in the serpulid and sabellariid. It colonizes first the right valves of the smaller scallops (group A) with a 0.6% dominance which progressively decreases to 0.4 % (group C). Moreover, *P. lebruni* predominantly settles on the umbonal region of both valves (Fig. 2). The other species of spirorbids are rare and are present only on the larger size groups.

Source : MNHN, Paris

## CONCLUSIONS

The frequency of polychaetes tends to increase from the smaller valves to the larger ones which follows the general trend of the other epibionts. However, the principle spirorbid species colonizes the smaller scallops, whereas the other polychaetes encrust only medium or large sized scallops. This could be due to different strategies depending on the species. Some species appear to be pioneer forms that colonize the newly available substrata (young pectinids), whereas others appear only when the community is already mature, on medium and large sized pectinids.

The larger serpulids and sabellariids colonize only the left upturned valves, a survival strategy related more to the size of their tubes, rather than to a phototropism. In contrast, the principle spirorbid species, which are abundant on the low profiled right valves, appear better adapted to the physical abrasion effects, in direct contact with the substratum. KNIGHT-JONES & KNIGHT-JONES (1984) also concluded that *P. lebruni* has the capacity of withstanding sand abrasion. This was hypothesized by WARD & THORPE (1991) for bryozoans. The spirorbid distribution was not homogeneous on the right valve, but showed a concentration towards the umbonal regions, particularly on the posterior side. The higher umbonal density may be due to more prolonged settlement, since this area has been available for colonisation for a longer period than the younger peripheral parts of the shell. It is unlikely to be related to the swimming of *Chlamys*. This is caused by two jets of water emitted from between the valves dorsally (MOORE & TRUEMAN, 1971), but swimming excursions are brief and very infrequent.

It seems possible that the asymmetrically posterior distribution of spirorbids may be related to the pattern of eddies set up by the excurrent stream from the *Chlamys* mantle cavity, which could conceivably bring in settling larvae and nutrients in suspension. Probably, moreover, much of the initial spirorbid settlement occurs during the juvenile stage, when the *Chlamys* is attached with the anterior side partially in contact with the substratum. The relative abundance of spirorbids on smaller *Chlamys* could be due to their having been recently in juvenile situations, with byssal attachments to larger rocks in shallower water, where spirorbids are more dominant (KNIGHT-JONESS, com. pers.) The much denser algal cover also suggests that they may have been recently in shallower water, although it must be admitted that algae are among the earliest colonisers of new surfaces.

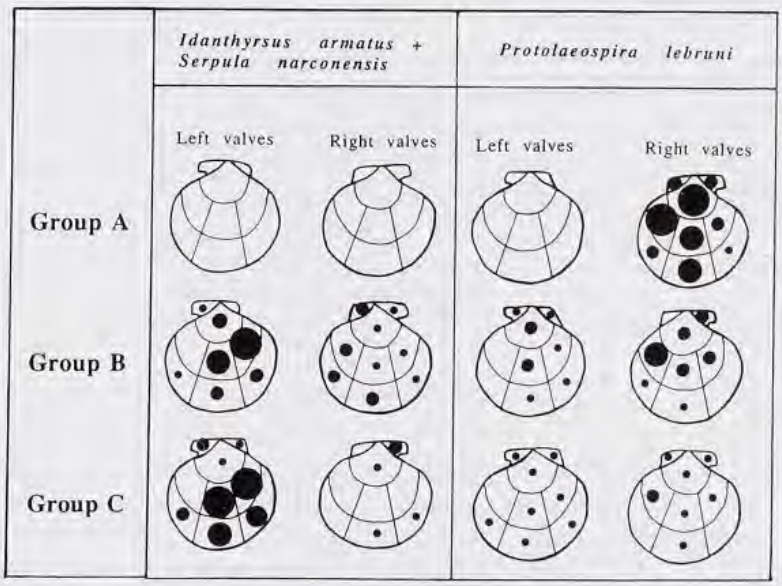



FIG. 1. — Diagrams showing changes in abundance of covering of some significant polychaetes species depending on shell size (covering percentage for each of the nine mapped areas).

• < 1 %
● = 1 % to 10 %
● = 10 % to 30 %
● > 30 %

Source : MNHN, Paris

## ACKNOWLEDGEMENTS

The author is grateful to Drs. P. and E.W. KNIGHT-JONES for help in identifying spirorbid species and for useful discussions; and to Prof. I. Di GERONIMO and Dr. A. ROSSO of the University of Catania for helpful suggestions; and to Caty STANDLEY, B.A. for linguistic help. Research financially supported by P.N.R.A. (Italian National Research Program in Antarctica), Biological Oceanographic Sector, Program on Benthic Communities, Unit of Catania, Responsible Prof. I. Di GERONIMO, paper n° 14.

## REFERENCES

BRAMBATI, A., FONTOLAN, G. & SIMEONI, U., 1991. — Recent sediments and sedimentological processes in the Strait of Magellan. *Boll. Oceanol.*, **9** : 217-259.

DI GERONIMO, I. & ROSSO, A., 1990. — First Italian Oceanographic Expedition in the Ross Sea, Antarctica. Benthos: a preliminary report. *Nat. Sc. Com. Ant., Ocean. Camp. 1987—88, Genoca, Data Report: (1990) 1* : 407-421.

DI GERONIMO, I., PRIVITERA, S. & VALDOVINOS, C., 1992. — Molluskan Thanatocoenoses of the Magellan Strait. *Mem. Biol. Mar. e Oceanogr.*, **19** : 205-208.

HARRIS, T., 1969. — Spirorbid species (Polychaeta: Serpulidae) from the South Atlantic. *Discovery Rep.*, **35** : 135-178.

HARTMAN, O., 1966. — Polychaeta Myzostomidae and Sedentaria of Antarctica. *Antarctic Res. Ser.*, **7** : 1-158.

KNIGHT-JONES, P. & KNIGHT-JONES, E.W., 1984. — Systematics, ecology and distribution of southern hemisphere Spirorbids (Polychaeta; Spirorbidae). *In:* P.A. HUTCHINGS (ed), *Proceedings of the First International Polychaete Conference*, Sydney. Linnean Society of New South Wales, Sydney : 197-210.

KNIGHT-JONES, P. & KNIGHT-JONES, E.W.,1991. — Ecology and distribution of Serpuloidea (Polychaeta) round South America. *Ophelia*, suppl. **5** : 579-586.

MOORE, J.D. & TRUEMAN, E.R., 1971. — Swimming of the scallop, *Chlamys opercularis* (L.). *J. exp. mar. Biol. Ecol.*, **6** : 179-185.

ROSSO, A. & SANFILIPPO, R., 1992. — Epibiont distribution pattern on *Chlamys patagonica* (King & Broderip) of the Magellan Strait. *Mem. Biol. Mar. e Oceanogr.*, **19** : 237-240.

WALOSZEK, D. & WALOSZEK, G., 1986. — Ergebnisse der Forschungreisen des FFS "Walther Herwig" nach Südamerika. LXV. Vorkommen, Reproduktion, Wachstum und mögliche Nutzabarkeit von *Chlamys patagonica* (King & Broderip, 1832) (Bivalvia, Pectinidae) auf dem Schelf vor Argentinien. *Arch. Fisch.-Wiss.*, **37** : 69-99.

WARD, M.A. & THORPE, J.P., 1991. — Distribution of encrusting bryozoans and other epifauna on the subtidal bivalve *Chlamys opercularis*. *Mar. Biol.*, **110** : 253-259.

Source : MNHN, Paris

# Polychaeta in the estuary of the Piauí River, Sergipe, Brazil

*Maria A. SANTOS, C.S.G. SANTOS & C.M.M. OLIVEIRA*

Departamento de Biologia
Campus Universitário
49000 Aracaju, Sergipe, Brasil

ABSTRACT

The distribution of infaunal polychaetes was examined in order to discriminate polychaete assemblages in the estuary. In March 1987, 4,398 specimens were collected in 123 samples from 15 areas. A cluster and ordination analysis was used to define benthic polychaete assemblages. Two associations were present which were related to the high and low energy depositional environments and hydrological gradients. The first group, restricted to the upper reaches of the estuary, was composed of *Laeonereis acuta*, *Amphicteis gunneri*, *Heteromastus similis*, *Neanthes succinea* and *Scolelepis texana*. The second group, present in the middle section of the estuary, was dominated by *Prionospio (P.)* cf. *dubia*, *Scoloplos* sp., *Euclymene* sp., *Isolda pulchella* and *Magelona papillicornis*.

RÉSUMÉ

**Polychètes de l'estuaire de la rivière Piauí, Sergipe, Brésil**

Cette étude porte sur la distribution de la faune des Polychètes de l'estuaire du fleuve Piauí. 4 398 spécimens furent récoltés en mars 1987, en 123 échantillons de 15 régions. L'analyse en composantes principales et la classification hiérarchique permettent de définir les assemblages des Polychètes benthiques. Deux groupes ont été identifiés: le premier est restreint à la partie amont de l'estuaire du Piauí; il est formé de *Laeonereis acuta*, *Amphicteis gunneri*, *Heteromastus similis*, *Neanthes succinea* et *Scolelepis texana*. Le deuxième groupe est présent dans la partie moyenne de l'estuaire, avec les espèces dominantes *Prionospio (P.)* cf. *dubia*, *Scoloplos* sp., *Euclymene* sp., *Isolda pulchella* et *Magelona papillicornis*.

## INTRODUCTION

The estuary of the Piauí River is located in the state of Sergipe, Brazil. A qualitative study of polychaetes was made off-shore (NONATO & LUNA, 1970 a, b) and in the Sergipe River Estuary (SANTOS, 1979) which provided information on the distribution of polychaetes and other animals. Studies were made in the Piauí-Fundo-Real system to characterize the region, according to physicochemical variations (ALVES, 1989), zooplankton (ARAUJO, 1989), sediment and Foraminifera distribution (ZUCON, 1989) and phytoplankton (FRANCO, 1991). Macrobenthic

SANTOS, M.A., SANTOS, C.S.G. & C.M.M. OLIVEIRA, 1994. — Polychaeta in the estuary of the Piaui River Sergipe, Brazil. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 541-547. Paris ISBN 2-85653-214-4

Source : MNHN, Paris

fauna studies in other estuarine regions of the Brazilian Coast have been made by BEMVENUT (1987), LANA (1986) and LANA *et al.* (1989). The objective of this paper is to describe the distribution and diversity of subtidal polychaetes in a tropical estuary located in northeast Brazil.

## STUDY AREA

The Piauí River is part of the estuarine complex, located in Sergipe, Brazil (11°22'30" S / 32°22'33" W) (Fig. 1). It is approximately 40 km long and 50-5,000 m in width. The depth ranges from 1-27 m (FRANCO, 1991). The water temperature ranged from 24 to 29.5 °C in 1986/87 (ALVES, 1989). The region is characterized by dry and wet periods. The rainfall ranges from 241.5 mm/month in July to 46.1 mm/month in December (ALVES, 1989). The sediment of the Piauí River varies from coarse sand poorly selected in the upper estuary to fine sand well selected at the mouth. The total granulometrical distribution has a median value of 2.5 (± 1.1) and varies from coarse sand to clay. The highest percentage of fine sand was 43.6 (ZUCON, 1989). The selection varies from 1.16 % well selected sediment to 53.18 poorly selected sediment. The areas 7 to 10 (Fig. 1) are characterized by biodetritus.

The salinity varies as a result of seasonal fluctuations of rainfall, river run-off, and tidal amplitude (FRANCO, 1991). These waters can be divided into three categories: 1) limnetic water from river flow in the upper part of the estuary, 2) mixohaline waters from the mixture of river and coastal water and 3) mixoeuhaline waters at the mouth of the river (ALVES, 1989).

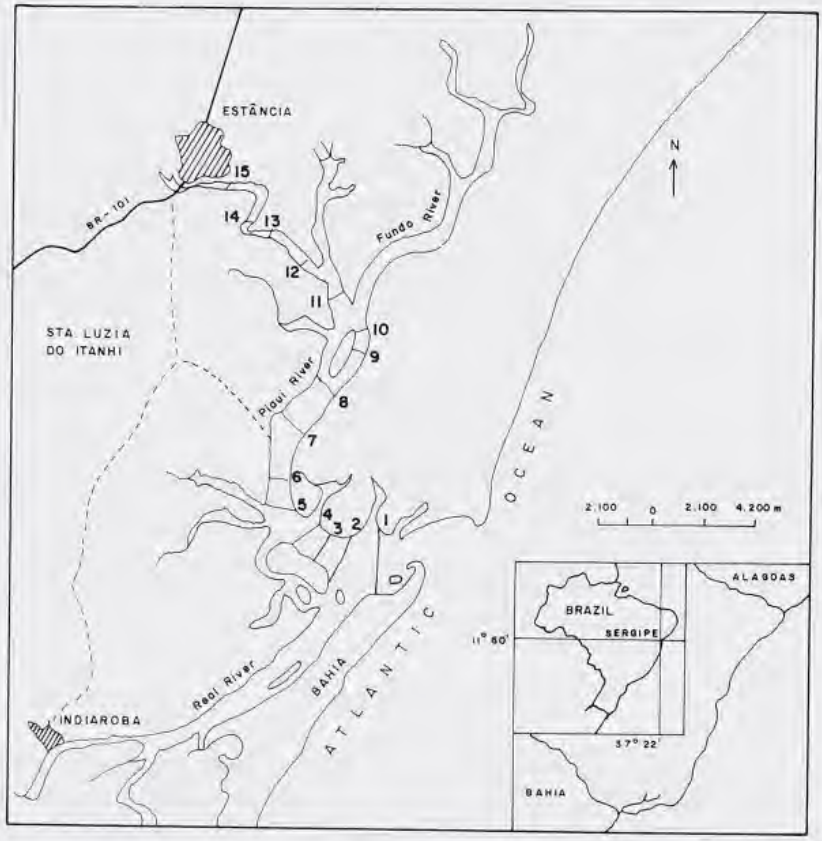



FIG. 1 — Piaui River, showing the position of the samplings areas.

Dissolved oxygen generally ranged from 2.2 to 6.8 mg. $l^{-1}$ (ALVES, 1989). The median estuarine region showed the highest level of nutrients, diatom density and zooplankton (ALVES, 1989; FRANCO, 1991; ARAUJO, 1989). The changes in nutrients are probably a consequence of the annual climatological and hydrographical pattern.

Source : MNHN, Paris

## MATERIAL AND METHODS

Samples were taken in March 1987. Fifteen areas were sampled along 35 km of the estuary (Fig. 1). A total of 123 samples were taken using a 10 liter Van Veen grab. Three stations were sampled in each area, and four replicates were taken at each station, one for sediment analysis and three for biological analysis. Only two stations were sampled in areas 12 - 15. Each biological sample was washed through a 0.5 mm sieve. Larger animals were picked from the sieve. Remaining material was stained with Bengal Rose and fixed in formalin. Samples were transferred to 70 % alcohol prior to identification. Environmental parameters and other biological aspects of the Piauí estuarine system were studied concurrently (ALVES, 1989; ARAUJO, 1989; FONTES, 1989; ZUCON, 1989; FRANCO, 1991).

The species were ranked according to occurrence, abundance and percentage of total number of specimens. The Shannon-Wiener diversity index and evenness indices were used (GRAY, 1981). A matrix data with the abundance of 80 species and 41 samples was used for the data analysis. The replicates were summed up by area for cluster and ordination analysis. The variables indicating abundance were logarithmically transformed using the expression $Y_{ij} = \log (x_{ij} + 1)$ (GREEN, 1979).

The matrix was subjected to a cluster analysis (WPGMA), employing the Czekanowski Coefficient of similarity. The multivariate similarity patterns were also studied with a Q-mode Principal Component Analysis (PCA). The analysis in Q mode was done because of the large number of species. A computer program ACOMP written by J. L. VALENTIN (IEAPM - MM) was used.

## RESULTS

A total of 4,398 specimens was collected which belonged to 81 taxa in 32 families. The dominant taxa were identified by occurrence and abundance. The most abundant species were *Prionospio (P.)* cf. *dubia*, *Laeonereis acuta*, *Euclymene* sp. and *Isolda pulchella* (Table 1). The diversity ranged from 0.01 to 2.8 and was higher from areas 2 to 10. The lowest value was found at areas 11 to 15 (Table 2).

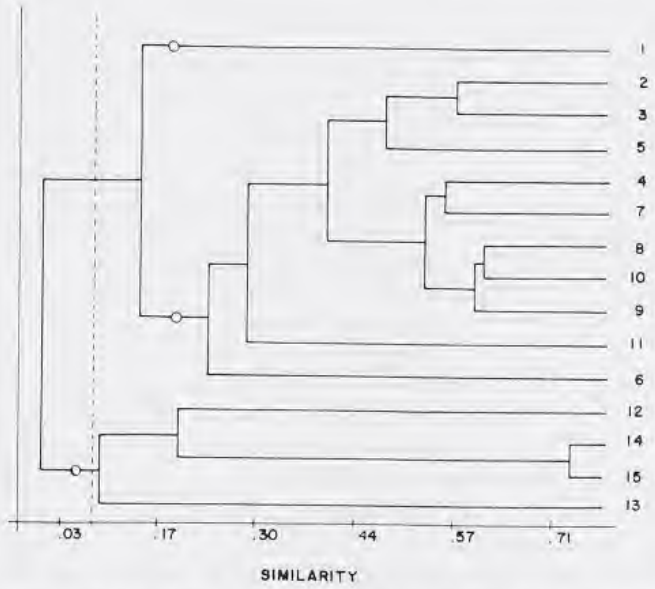



FIG. 2. — Dendrogram for 80 species of polychaetes, considering 15 areas. The abundance of the species was summed up in each area.

Cluster analysis indicated: 1) Area 1 at the mouth of the river is euhaline and is separated from the others. The salinity was about 35,0 ‰, and the sediment was principally well sorted fine sand. 2) Areas 2 to 11 were clustered together with two groups: areas 2, 3, 5 and 4, 7, 8, 9, 10, 11. The salinity ranged from 18-30, P.S.U. and the

Source : MNHN, Paris

TABLE 1. — Rank and abundance of the most common polychaetes taxas collected in the Piauí River, Sergipe.

| Species | Rank | Occurrence (n°) | Numbers for survey (Total) | % of total |
|---|---|---|---|---|
| *Scoloplos sp.* | 1 | 51 | 207 | 4.70 |
| *Prionospio (P.) cf. dubia* | 2 | 45 | 593 | 13.48 |
| *Isolda pulchella* | 3 | 36 | 352 | 8.00 |
| *Tharyx* sp. | 4 | 35 | 63 | 1.43 |
| *Ceratocephala crosslandi* | 5 | 35 | 134 | 3.04 |
| *Euclymene* sp. | 6 | 27 | 447 | 10.16 |
| *Poecilochaetus australis* | 7 | 26 | 173 | 3.93 |
| *Goniada maculata* | 8 | 23 | 47 | 1.00 |
| *Magelona papillicornis* | 9 | 23 | 278 | 6.32 |
| *Laeonereis acuta* | 10 | 23 | 1168 | 26.55 |
| *Sigambra grubii* | 11 | 22 | 32 | 0.72 |
| *Polycirrus* cf. *plumosus* | 12 | 21 | 74 | 1.68 |
| *Magelona nonatoi* | 13 | 18 | 29 | 0.65 |
| *Neanthes succinea* | 14 | 16 | 43 | 0.24 |
| *Stauronereis rudolphi senso* | 15 | 16 | 24 | 0.54 |
| *Cabira* cf. *incerta* | 16 | 15 | 35 | 0.79 |
| *Trochochaeta* sp. | 17 | 15 | 156 | 3.54 |
| *Diopatra* A | 18 | 15 | 41 | 0.93 |
| *Diopatra* B | 19 | 13 | 22 | 0.50 |
| *Glycera* sp. A | 20 | 12 | 14 | 0.31 |
| *Pista corrientis* | 21 | 12 | 15 | 0.34 |
| *Magelona variolamellata* | 22 | 12 | 33 | 0.75 |
| *Pectinaria catharinensis* | 23 | 12 | 13 | 0.29 |
| *Sternaspis capillata* | 24 | 11 | 24 | 0.54 |
| *Malacoceros vanderhorsti* | 25 | 11 | 17 | 0.38 |
| *Parandalia tricuspis* | 26 | 10 | 22 | 0.50 |
| *Amphicteis gunneri* | 27 | 10 | 26 | 0.59 |
| *Pectinaria catharinensis* | 28 | 10 | 13 | 0.29 |
| *Marphysa* sp. | 29 | 10 | 10 | 0.22 |
| *Kinbergonuphis* spp. | 30 | 10 | 10 | 0.22 |
| *Scolelepis* sp. | 31 | 9 | 15 | 0.34 |
| *Hemipodus* B | 32 | 9 | 24 | 0.54 |
| *Glycera americana* | 33 | 8 | 10 | 0.22 |
| *Glycinde multidens* | 34 | 8 | 9 | 0.20 |
| *Magelona posterolongata* | 35 | 6 | 6 | 0.13 |
| *Laonice* sp. | 36 | 6 | 8 | 0.18 |
| *Heteromastus similis* | 37 | 6 | 9 | 0.20 |
| *Owenia fusiformis* | 38 | 6 | 8 | 0.18 |
| *Chone* sp. | 39 | 5 | 12 | 0.27 |
| *Spiophanes* sp. | 40 | 4 | 30 | 0.68 |
| *Loimia medusae* | 41 | 4 | 5 | 0.11 |
| *Eunoe* sp. | 42 | 4 | 7 | 0.15 |
| *Lysidice* sp. | 43 | 4 | 7 | 0.15 |
| *Branchiomma nigromaculata* | 44 | 3 | 7 | 0.15 |
| *Pectinaria laelia* | 45 | 3 | 3 | 0.06 |
| *Sthenolepis grubei* | 46 | 3 | 5 | 0.11 |
| Others | 50 | - | 118 | 2.68 |
| TOTAL | | | 4.398 | |

Source : MNHN, Paris

sediment ranged from sand to silt and clay and was characterized for biodetritus in areas 7 to11. 3) Areas 12 to 15 were characterized by salinity ranging from 1 to,15 P.S.U., going from mesohaline to oligohaline zones. The sediment was mostly coarse sand.

TABLE 2. — Diversity and evenness values

| Areas | Diversity | Evenness | Areas | Diversity | Evenness |
|---|---|---|---|---|---|
| 1 | 2.14395 | 0.97575 | 9 | 2.46250 | 0.70427 |
| 2 | 2.67771 | 0.85400 | 10 | 2.16672 | 0.60005 |
| 3 | 2.44909 | 0.70044 | 11 | 2.47467 | 0.84045 |
| 4 | 2.88888 | 0.75890 | 12 | 1.04351 | 0.75274 |
| 5 | 2.00215 | 0.66833 | 13 | 0.66225 | 0.47771 |
| 6 | 2.52725 | 0.75843 | 14 | 0.24756 | 0.17858 |
| 7 | 2.39059 | 0.63959 | 15 | 0.01851 | 0.02670 |
| 8 | 2.18262 | 0.60002 | TOTAL | 2.79627 | 0.63812 |

These groups of areas, clustered together, were partially influenced by changes in polychaete density. However, these results divided the Piauí River in 3 regions: the mouth, area 1, the lower estuary, area 2 to 11 and the upper estuary, area 12 to 15.

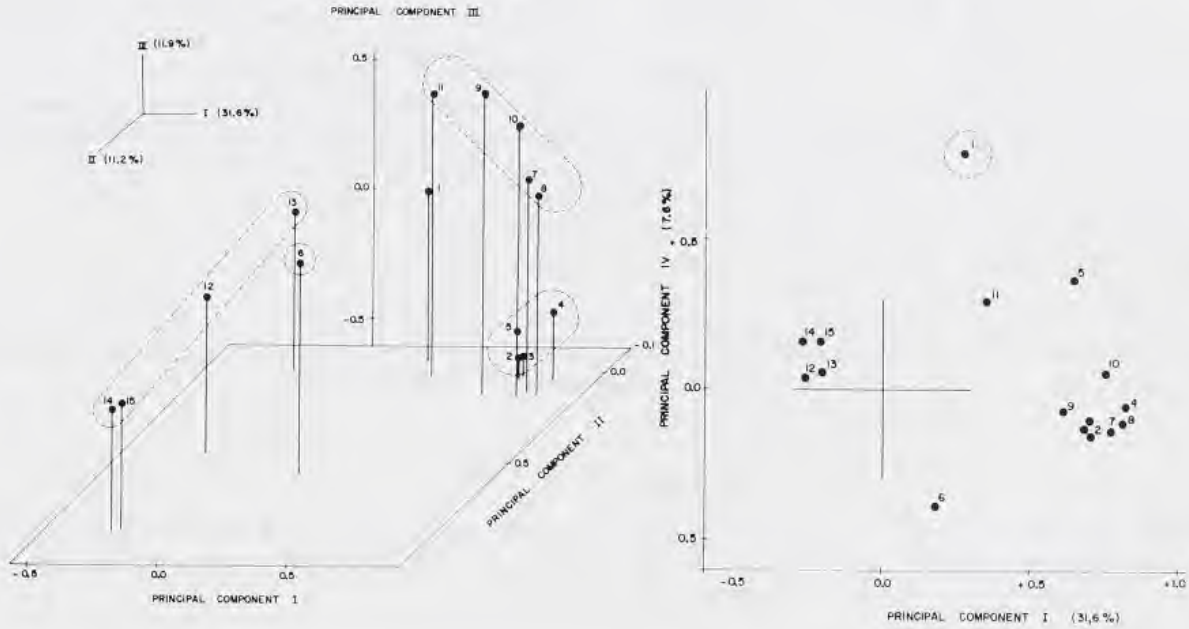



FIG. 3. — Position of 15 areas on principal components: left, I, II and III; right, I and IV showing principally area 1.

By projecting the scores in the orthogonal space of the first three principal components (Fig. 3A), it was possible to see that groups of stations were perfectly discriminated. The first axis was related to the abundance of *Prionospio (P.)* cf. *dubia*, *Scoloplos* sp., *Euclymene* sp., *Isolda pulchella* and *Ceratocephala crosslandi*, indicating the most similar areas from 2 to 11 divided into two groups: 2 to 5 and 7 to 11. The second axis was

Source : MNHN, Paris

related to the abundance of *Laeonereis acuta*, *Amphicteis gunneri*, *Scolelepis texana*, *Hemipodus* sp. in areas 12 to 15. The fourth axis was probably related to the negative abundance of species (Fig. 3B). Almost the same groups were obtained by cluster analysis: area 1 isolated, areas from 2 to 11 clustered together and areas 12 to 15 clustered together (Fig. 2).

## DISCUSSION

Tropical estuaries are influenced by the seasonal rain pattern and the resulting effects due to sedimentation, erosion, dissolved oxygen and nutrients. Nearly all the benthic surveys of tropical estuaries have been taken along the east and west coast of India, (ALONGI, 1990). The most extensive investigations of subtropical estuarine macrobenthos were near Brisbane in Queensland, Australia (STEPHENSON *et al.*, 1972; STEPHENSON *et al.*, 1977). STEPHENSON *et al.* (1972) stated that workers in the subtropics and tropics failed to find communities with only a few dominant species.

MAURER & VARGAS (1984) found a depauperated infauna in the soft bottom benthos in the Gulf of Nicoya, Costa Rica. They concluded that tropical estuarine communities were generally low in density and biomass. The mean Shannon-Wiener diversity for polychaetes was of 1.91, range = 0 to 3.09 (MAURER *et al.* 1988).

In the Piaui River the diversity was similar to the values found in Costa Rica (MAURER*et al*, 1988). The influence of industrial wastes in the Piauí River estuary could be considered as a factor causing the low diversity. Comparison of the polychaetes obtained in the Piauí River estuary and the Sergipe estuary in the northeastern region of Brazil (SANTOS, 1979) showed the same pattern of species composition and species abundance.

Zones of changes occurred in the Piauí River, and it was possible to divide the river in three region, the mouth, the lower estuary and the upper estuary. Similar regions were found in foraminiferan studies of Piaui River (ZUCON, 1989) and macrobenthic studies of Sergipe River (SANTOS, 1979).

The upper part of the Piauí Estuary, areas 12 to 15, was dominated by *L. acuta* and *A. gunneri*. The occurrence of *L. acuta* as dominant species, in the upper river, was observed in Sergipe Estuary (SANTOS, 1979). The occurrence of *L. acuta* and *H. similis* association in the upper river was also observed in the southeastern coast of Brazil (LANA, 1986; BEMVENUTI, 1987). These species are euryhaline with reduced mobility.

In the lower estuary areas 2 to 11 with mixohaline waters, the greatest abundance of polychaetes, plankton and nutrients were present (ALVES, 1989; FRANCO, 1991). This suggested that the benthic population distribution was influenced not only by salinity and sediment but also for nutrients and productivity (ALONGI, 1990). The occurrence of *Prionospio (P.)* cf. *dubia*, *Scoloplos* sp., *Euclymene* sp., *Isolda pulchella* and *Ceratocephala crosslandi* association was also found in Sergipe Estuary (SANTOS, 1979).

Area 1 was located at the mouth of the estuary, in a region of continuous sedimentation, and was separated from the others by cluster and PC analysis.

The pattern of distribution of the polychaetes in the Piauí River are directly influenced by the physicochemical gradients, sediment types and by topography. It is possible to notice groups of dominant species in each one of the three regions, and the decrease of the diversity from the mouth to the head of the estuary.

## ACKNOWLEDGEMENTS

We are grateful to M Sc C. R. P. Franco for critically reading the manuscript, to Dr. Paulo da C. LANA for help us in polychaete identification and A. F. Diniz for ordenation analysis. This study was supported through grant from the Interministry Commission for Marine Resources.

## REFERENCES

ALVES, J. P. H., 1989. — Projeto integrado para avaliação da potencialidade do estuário dos rios Piauí-Fundo-Real: Vol. II. Características físico-químicas da água e comportamento dos nutrientes. *Report*, Aracaju/SE, UFS, 43p.

ALONGI, D. M., 1990. — The ecology of tropical soft-bottom benthic ecosystems. *Oceanogr. mar. Biol. Ann. Rev.*, **28** : 381-496.

ARAUJO, H. M. P., 1989. — Projeto integrado para avaliação da potencialidade do estuário dos rios Piauí-Fundo-Real: Vol. III. Biomassa do zooplancton. Report, Aracaju/SE, UFS, 130 pp.

Source : MNHN, Paris

BEMVENUTI, C. E., 1987. — Macrofauna bentônica da região estuarial da Lagoa dos Patos, RS, Brasil - Simpósio sobre ecossistemas da costa sul e sudeste brasileira. *Publ. ACIESP*, **54** : 428-459.

FONTES, A. L., 1989. — Projeto integrado para avaliação da potencialidade do estuário dos rios Piauí-Fundo-Real: Vol. I. Caracterização geomorfológica da bacia do Mangue Seco (Piauí-Fundo-Real). *Report*, Aracaju/SE, UFS, 22 pp.

FRANCO, C. R. P., 1991. — *Plancton diatoms of the Piauí river estuary (Brazil): seasonal distribution and biogeographic affinities*. Master Thesis, University of Rhode Island, Kingston, 169 pp.

GRAY, J. S., 1981. — *The ecology of marine sediments*. Cambridge University Press, London, 185 pp.

GREEN, R. H., 1979. — Sampling design and statistical methods for environmental biologists, John Wiley & Sons, New York, 257 pp.

LANA, P. C., 1986. — Macrofauna bêntica de fundos sublitorais não consolidados da Baía de Paranaguá (Paraná). *Nerítica*, **1** : 79-89.

LANA, P. C., ALMEIDA, M. V. O., FREITAS, C. A. F., COUTO, E. C. G., CONTI, L. M. P., GONZALEZ-PERONTI, A. L., GILES, A.G., LOPES, M. J. S., SILVA, M. H. C. & PEDROSO, L. A., 1989. — Estrutura espacial de associações macrobênticas sublitorais da Gamboa Perequê (Pontal do Sul, Paraná). *Nerítica*, **4** : 129-136.

MAURER, D. & VARGAS, J. A., 1984. — Diversity of soft-bottom benthos in a tropical estuary: Gulf of Nicoya, Costa Rica. *Mar. Biol.*, **81** : 97-106.

MAURER, D., VARGAS, I. A. & DEAN, H., 1988. — Polychaetous annelids from the Gulf of Nicoya, Costa Rica. *Int. Rev. Gesamten Hydrobiol.*, **73** : 43-59.

NONATO, E. F. & LUNA, J. A. C., 1970a. — Sobre alguns poliquetas de escama do Nordeste do Brasil. *Bolm. Inst. Oceanogr.*, São Paulo, **18** : 63-91.

NONATO, E. F. & LUNA, J. A. C., 1970b. — Anelideos poliquetas do Nordeste do Brasil. I. Poliquetas bentônicos da costa de Alagoas e Sergipe. *Bolm. Inst. Oceanogr.*, São Paulo, **19** : 57-130.

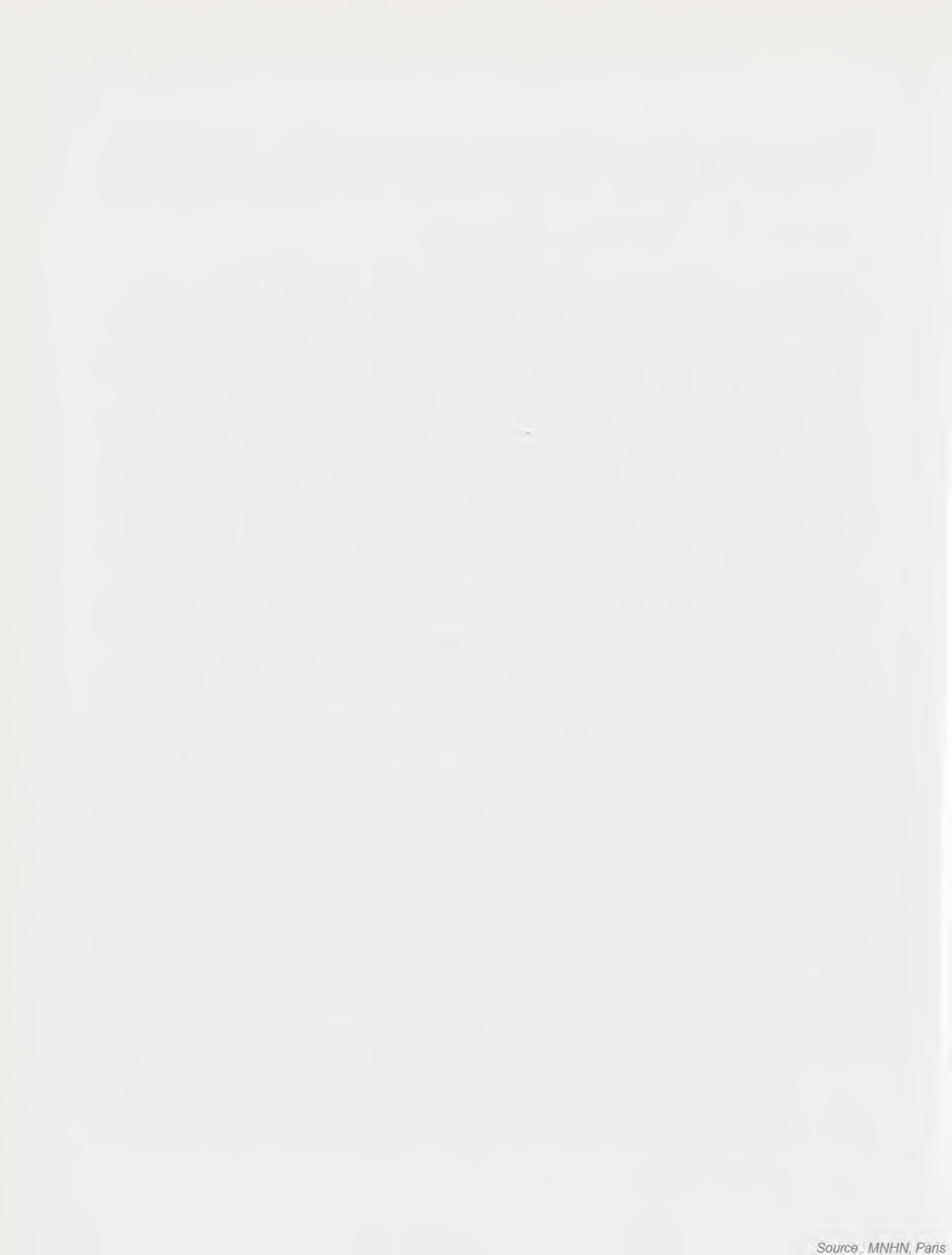
SANTOS, M. A., 1979. — *Macrofauna bêntica do estuário do Rio Sergipe (Estado de Sergipe, Brasil)*. Doctor Thesis, Universidade de São Paulo. São Paulo, 128 pp.

STEPHENSON, W., COOK, S. D. & RAPHAEL, Y. I., 1977. — The effect of a major flood on the macrobenthos of Bramble Bay, Queensland. *Mem. Queensl. Mus.*, **18** : 95-119.

STEPHENSON, W., WILLIAMS, W. T. & COOK, S. D., 1972. — Computer analyses of Petersen's original data on bottom communities. *Ecol. Monogr.*, **42** : 387-409.

ZUCON, M. H., 1989. — *Distribuição dos foraminíferos e tecamebas do estuário do rio Piauí-Sergipe*. Master Thesis, Universidade Federal do Paraná, Curitiba, 54 pp.

Source : MNHN, Paris



Source : MNHN, Paris

# Life history of the Polychaete *Polydora variegata* that bores into the shells of Scallops in Northern Japan

*Waka SATO-OKOSHI*

Laboratory of Biological Oceanography
Faculty of Agriculture, Tohoku University
Sendai 981, Japan

ABSTRACT

The genus *Polydora* (Polychaeta, Spionidae) is widely known for its boring activities in molluscan shells. Here we describe the life history of *Polydora variegata*, which causes considerable damage to scallops sown in the waters of Abashiri Bay, off the Okhotsk Sea coast of Hokkaido, Japan, by spreading blisters and penetrating the shells. The life span of *P. variegata* was 2.5 years after settlement, and the main spawning period of both 0- and 1-yr-olds was from August to October. Three-setiger larvae hatched from the egg capsule mainly from September through November. Settlement of 17-setiger larvae took place during the drift-ice period. There was a tendency for the earliest settlement of *P. variegata* to occur on a narrow band around the periphery of the left valve of the scallops. A large body size, high reproductive activity and a long life span seem to be characteristic of this species of boring polychaete.

RÉSUMÉ

**Cycle de vie du Polychète *Polydora variegata*, espèce perforante des Coquilles Saint Jacques dans le nord du Japon**

Le genre *Polydora* (Polychètes, Spionidae) est bien connu pour ses activités de perforation des coquilles de mollusques. Ce travail décrit le cycle de vie de *Polydora variegata*, espèce qui cause des dommages considérables aux coquilles Saint-Jacques de la baie d'Abashiri, au large des côtes d'Hokkaido, en mer d'Okhotsk, Japon, par l'étendue des boursouflures et la pénétration des vers dans l'épaisseur des coquilles. La durée de vie de *P. variegata* est de deux ans et demi après la fixation, et la principale période de reproduction pour les deux groupes d'individus d'âge 0 et d'âge 1 s'étend d'août à octobre. Les larves à trois sétigères sortent de la capsule de l'oeuf principalement de septembre à novembre. La fixation des larves à 17 sétigères se situe au moment de la débacle des glaces. On a noté une tendance des *P. variegata* à se fixer d'abord sur une bande étroite autour de la périphérie de la valve gauche des coquilles Saint-Jacques. Une grande taille corporelle, une activité reproductrice élevée et une longue durée de vie semble être les caractéristiques de cette espèce de polychète perforante.

---

SATO-OKOSHI, W., 1994. — Life History of the Polychaete *Polydora variegata* that bores into the shells of Scallops in Northern Japan *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 549-558. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

## INTRODUCTION

The spionid genus *Polydora* is found in a wide variety of substrates that range from soft clays or mud to hard calcareous materials (BLAKE & EVANS, 1972). The life history and population dynamics of the genus have been discussed by DORSETT (1961), DARO & POLK (1973), GUDMUNDSSON (1985), and ZAJAC (1992). Nearly all the previous studies have dealt with *Polydora* that inhabit soft-bottom habitats, but there have been only few studies on dealing with those species which bore into shells.

Infestation by *Polydora* of commercially important molluscan shells is an important problem in aquaculture. *Polydora* not only reduces the value of molluscs but causes considerable damage to the shell, especially those in cultures. The species that bore into the shells of *Patinopecten yessoensis* do not feed on the host's tissue; the shell is used only as a refuge (SATO-OKOSHI & OKOSHI, 1992). Therefore, the polychaete is an inhabitant of the molluscan shell and not a parasite. Nonetheless, some worms do penetrate the inner surface of the shell and induce secretion by the shell of a thin layer of a dark or black organic material. Natural scallops with sufficiently thick shells suffer little damage even with heavy penetration by *Polydora*. However, cultured scallops have thin shells, a low growth rate and as a result, considerable damage when subjected to a heavy infestation by *Polydora*.

The Okhotsk Sea coast of Hokkaido is well known for its natural supply of scallops. Sowing of cultures was started in the waters of Abashiri Bay in 1977 in order to counteract the instability of the natural population. In these cultures, worms were observed to bore into the left valves, an average of 162 per shell; a maximum of 327 worms per shell have been counted (SATO, 1988). Very few worms bored into the right valve. The reproductive characteristics of *Polydora variegata* have been reported by SATO-OKOSHI *et al.* (1990). Details of its infestation and the nature of the burrows have been characterized for population in Abashiri Bay and elsewhere (MORI *et al.*, 1985; SATO-OKOSHI & NOMURA, 1990). The present study summarizes the life history of *P. variegata* in Abashiri Bay where it causes considerable damage to the scallops.

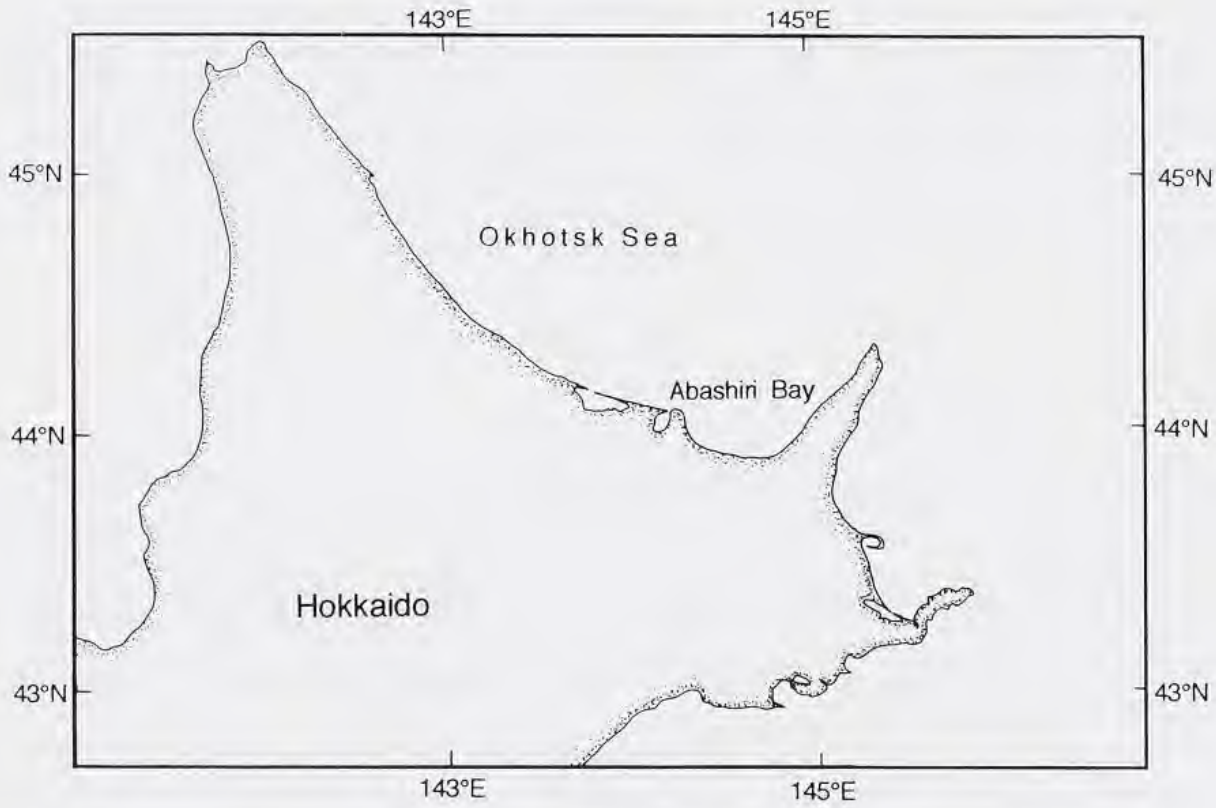



FIG. 1. — Location of sampling area.

Source : MNHN, Paris

## MATERIALS AND METHODS

Three- to five-year-old scallops were collected monthly by dredging from April 1982 to December 1986 (excluding 1985) from a depth of 30 to 50 m in Abashiri Bay, on the Okhotsk Sea coast of Hokkaido, Japan (Fig. 1). The scallops collected in 1982-1984 were the same cohort and their juveniles were collected in 1979 and sown in 1980, and scallops collected in 1986 were sown in 1984 from their juveniles collected in 1983. Two to 11 scallops were examined each month.

The scallop flesh was removed, and the left valve was broken into small pieces with pliers, and *P. variegata* were removed with forceps under a stereomicroscope. The presence of gametocytes was checked by rupturing segments and transferring the coelomic contents onto a microscope slide. Body size was determined by measuring the width of the fifth setiger after fixation in a neutralized 10 % solution of formalin.

Egg capsules were collected from the burrows of adults. The egg capsules were carefully removed from the burrows with forceps and placed in culture dishes that contained filtered seawater. After hatching from the egg capsule, larvae were maintained in 200-300 ml of filtered seawater in glass beakers at 12 °C. Larval development was observed under a stereomicroscope until settling and metamorphosis. The seawater was changed every 3-5 days. Larvae were fed a mixture of *Skeletonema costatum* and *Chaetoceros* spp. taken from Onagawa Bay.

## RESULTS

SETTLEMENT PATTERNS AND SIZE-FREQUENCY DISTRIBUTIONS. — Strong growth-inhibition rings were found on the shells of 4-year-old cultured scallops that had been sown in Abashiri Bay (Fig. 2). These rings corresponded to the times at which (1) scallops had been sown in June (R1); (2) the first winter season (R2); (3) the second winter season (R3); etc. (SATO-OKOSHI *et al.*,1990). In the winter season, the Okhotsk Sea coast of Hokkaido is generally covered with drift ice from January to March and referred to as the "drift-ice period".

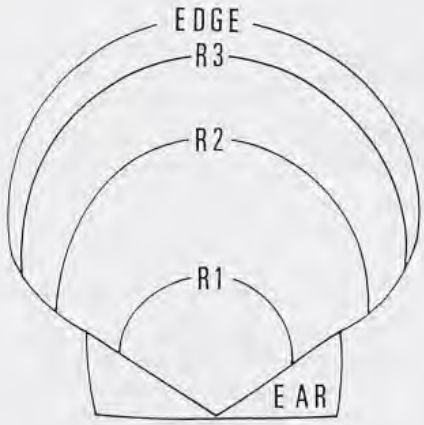



FIG. 2. — Growth-inhibition rings of scallops collected from Abashiri Bay. R1: Ring formed when scallops were sown in June; R2: ring formed during the first winter season; R3: ring formed during the second winter season (from SATO-OKOSHI *et al.*, 1990)

Size distributions of *P. variegata* in 1982, 1983, 1984 and 1986 are shown in Figure 3. A large number of *P. variegata* were observed to have bored around the inhibition rings, R2, R3 and R4, of the left valves. The size of the worms from each inhibition ring was investigated. The width of the fifth setiger was used as an index of the age of the worms (MORI *et al.*, 1985).

Source : MNHN, Paris

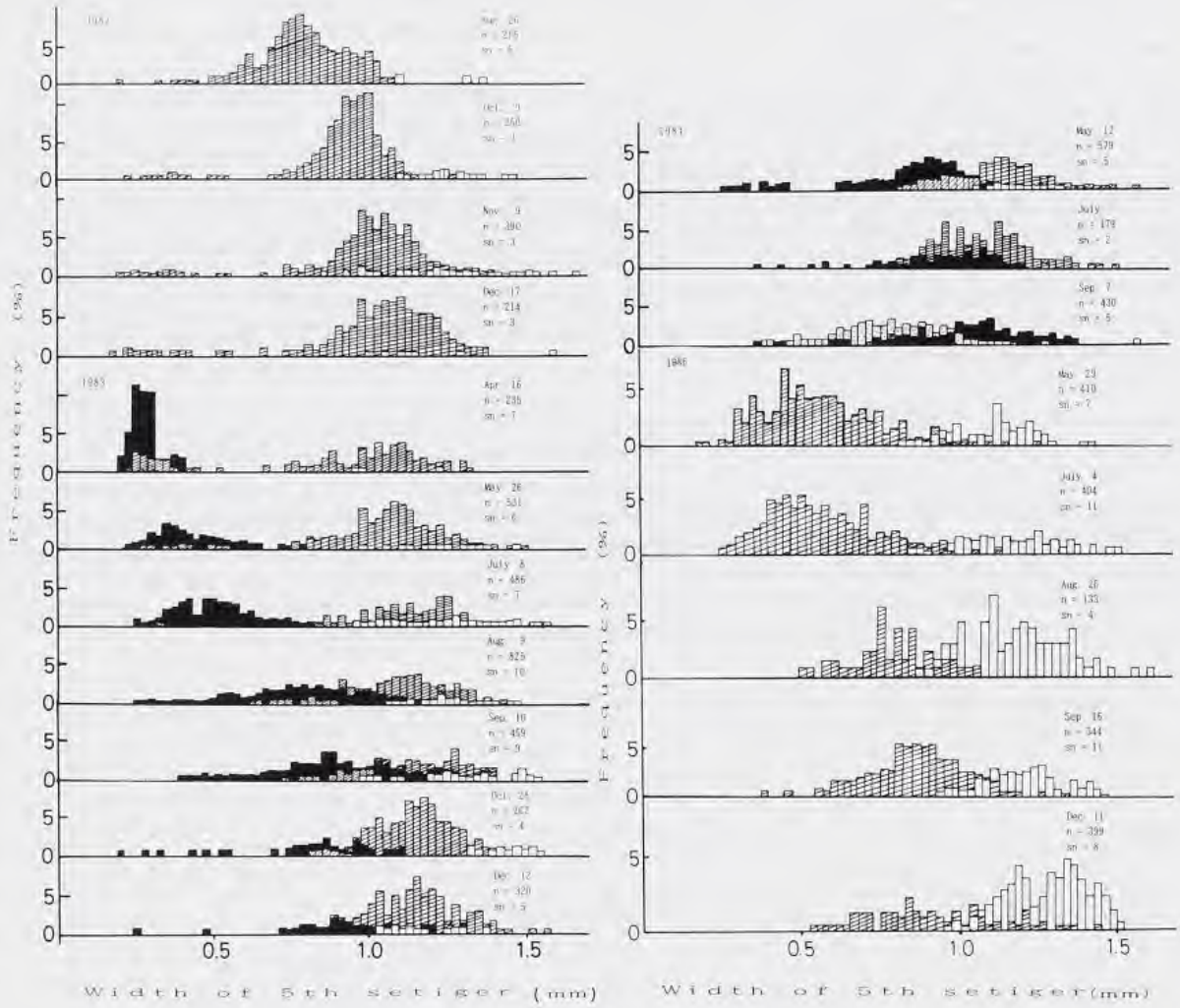



FIG. 3. — (1) on the left, (2) on the right. Size-frequency distributions of *Polydora variegata* that had bored into the left valves of scallops from April 1982 to December 1986 (excluding 1985). The worms in 1982-1984 were extracted from a population of scallops of the same age (juveniles collected in 1979 and sown in 1980). The worms in 1986 were extracted from scallops that had been sown in 1984 (juveniles collected in 1983). ▭, individuals that settled around R2; ▨, individuals that settled around R3; ■, individuals that settled around R4; ⁝⁝⁝, individuals that settled around R5. (adapted from MORI *et al.*, 1985 and from SATO-OKOSHI *et al.*, 1990). n, number of *P. variegata* examined; sn, number of scallop shells examined.

Source : MNHN, Paris

Young juveniles of about 20 segments appeared around the periphery of the left valve in April, after the drift-ice period. This observation suggests that the peripheral regions of the left valve during the drift-ice period subsequently become growth-inhibition rings, and that worms that settled on the peripheral regions grew around the inhibition rings. Thus, if both the age of the scallop and the boring region of the worms are known, it is possible to estimate the age of *P. variegata* individuals.

Worms around R3 appeared to have settled on the peripheral regions of the left valve during the period when the bay was frozen in 1982, while worms around R4 appeared to have settled on the peripheral regions during the same period in 1983.

The worms that settled on R3 in the drift-ice period of 1982 seemed to survive until the summer of 1984 but had disappeared by September. Thus, the life span of *P. variegata* seems to be approximately 2.5 years after settlement on a shell. The widths of the fifth setiger of newly settled worms varied from about 0.2 to 0.3 mm in April and grew to approximately 1.0 mm in December, about eight months after settlement. Once they had reached 1.0 mm in width, the worms grew slowly. The width of the fifth setiger did, however, varied from 0.8 mm to 1.5 mm in the second summer.

There was a small influx of newly settled worms around R3 throughout the period from August to December, 1982 (Fig. 3). Furthermore, some small worms found around R3 in April 1983 were obviously the newly settled young of 1983, demonstrating that, while almost all the juveniles settled around the peripheral region of the left valve, some settled around the other rings.

The same tendency was observed in 1986. Newly settled worms of 1986 during the drift ice period were observed to grow around R3 (0-year-olds) and larger worms which appeared to have settled in 1985 were observed to grow around R2 (1-year-olds).

From the data for 1982-1986, there seemed to be some years in which there was no settlement, for example, the winter of 1981. No worms were observed to settle around R2 in spite of the large number of worms around R3 and R4. These results suggest that the number of worms that settle on a shell fluctuates annually.

REPRODUCTION. — The reproductive patterns of 0- and 1-year-olds have been described previously (SATO-OKOSHI *et al.*, 1990). Table 1 shows the number and percentage of worms that contained gametocytes in the coelom and egg capsules in tubes in 1983 and 1986. Oocytes in the coelom of the female were shaped like an oval disc with the diameter of the long axis measuring 30 to 170 µm. Diameters of 130 to 140 µm were common in August in 0-year-olds and those of 130 to 140 µm were common in May to September in 1-year-olds in 1986 (SATO-OKOSHI *et al.*, 1990).

The proportion of worms that contained gametocytes increased to above 70 % among 0-year-olds in September and October, as the seawater temperature increased to 16-17 °C at a depth of 30 m. Some 0-year-olds measuring at least 0.6 mm wide contained gametocytes in the coelom, and females produced egg capsules. Brooding females appeared among the large worms of more than 0.8 mm in width in August and September, with an increase in October. Plural number of egg capsules made an egg string, and each egg string contained about 300 to 1,000 eggs. When the drift-ice period ended, almost all the 1-year-olds contained mature gametocytes. They were found in almost all the 1-year-olds throughout the year with a higher proportion of brooding females. Previous reports have indicated that the main reproductive season is from August to October (MORI *et al.*, 1985; SATO-OKOSHI *et al.*, 1990). Egg strings were observed throughout the year. Females seemed to have the potential for producing egg string repeatedly, with about 800 to 5,700 eggs produced per batch, during the period from August to October predominantly. The relationships between the width of the fifth setiger of the brooding female and the number of eggs per egg string for 0-year-olds and 1-year olds are, respectively, as follows:

$\ln Y = -1.10 \ln X + 7.80$ ($r^2 = 0.092$, $n = 7$) and $\ln Y = 1.05 \ln X + 6.19$ ($r^2 = 0.082$, $n = 25$) [X, width of 5th setiger (mm); Y, no. of eggs/string].

LARVAL DEVELOPMENT. — Larvae remained in the capsules until the three-setiger stage at which time they hatched. The time from the initial deposition of eggs to hatching was approximately 2 weeks at 15 °C. The long diameter of the oval fertilized egg was 150-160 µm with an average of 152.5 ± 11.0 µm. Asetigerous larvae measured 160 to 230 µm in length. Large macromeres filled the central portion of each larva. Two small circular eye spots were located dorsally. The larvae elongated and one or two distinct setigerous segments appeared. One- and two-setiger larvae measured 220-240 µm and 230-280 µm in length, respectively. Both early and late three-setiger larvae (Fig. 4A-B ) were positively phototactic. Yolk was still present within the gut. Four eyes were located on the dorsal surface of the head. Black pigmentation was seen on the dorsal surface of the third setiger and at the posterior end. Both the number and the length of the setae increased as this larval stage grew.

Source : MNHN, Paris

TABLE 1. — Numbers and frequencies of sexually mature worms of *Polydora variegata* in Abashiri Bay in 1983 and 1986. Numbers in parentheses show the frequency (%).

| Date | Total n° | Mature males | Mature females | Mature and mature males | females | Brooding females | Total females |
|---|---|---|---|---|---|---|---|
| **(a) 0-yr-olds** | | | | | | | |
| 83 Apr. 16 | 108 | 0 | 0 | 0 | | 0 | |
| May 26 | 106 | 0 | 0 | 0 | | 0 | |
| July 8 | 173 | 26 (15.0) | 13 (7.5) | 39 | (22.5) | 0 | |
| Aug. 9 | 280 | 110 (39.3) | 63 (22.5) | 173 | (61.8) | 4 | (6.3) |
| Sep. 10 | 151 | 73 (48.3) | 42 (27.8) | 115 | (76.2) | 10 | (23.8) |
| Oct. 28 | 46 | 18 (39.1) | 19 (41.3) | 37 | (80.3) | 7 | (36.8) |
| Dec. 12 | 42 | 15 (35.7) | 15 (35.7) | 30 | (71.4) | 0 | |
| 86 May 29 | 314 | 16 (5.1) | 8 (2.5) | 24 | (7.6) | 0 | |
| July 4 | 300 | 27 (9.0) | 10 (3.3) | 37 | (12.3) | 0 | |
| Aug. 26 | 48 | 17 (35.4) | 9 (18.8) | 26 | (54.2) | 2 | (22.2) |
| Sep. 16 | 232 | 111 (47.8) | 62 (26.7) | 173 | (74.6) | 8 | (12.9) |
| Dec. 11 | 208 | 87 (41.8) | 50 (24.0) | 137 | (65.9) | 0 | |
| **(b) 1-yr-olds** | | | | | | | |
| 83 Apr. 16 | 93 | 35 (37.6) | 30 (32.3) | 65 | (69.9) | 1 | (3.3) |
| May 26 | 370 | 153 (41.4) | 151 (40.8) | 304 | (82.2) | 18 | (11.9) |
| July 8 | 219 | 106 (48.4) | 100 (45.7) | 206 | (94.1) | 13 | (13.0) |
| Aug. 9 | 349 | 154 (44.1) | 170 (48.7) | 324 | (92.8) | 48 | (28.2) |
| Sep. 10 | 215 | 102 (47.4) | 102 (47.4) | 204 | (94.9) | 44 | (43.1) |
| Oct. 28 | 141 | 69 (48.9) | 66 (46.8) | 135 | (95.7) | 23 | 34.8) |
| Dec. 12 | 207 | 95 (45.9) | 93 (44.9) | 188 | (90.8) | 0 | |
| 86 May 29 | 100 | 50 (50.0) | 42 (42.0) | 92 | (92.0) | 1 | (2.4) |
| July 4 | 104 | 52 (50.0) | 52 (50.0) | 104 | (100) | 0 | |
| Aug. 26 | 87 | 39 (44.8) | 48 (55.2) | 87 | (100) | 19 | (39.6) |
| Sep. 16 | 158 | 72 (45.6) | 83 (52.5) | 155 | (98.1) | 43 | (51.8) |
| Dec. 11 | 209 | 109 (52.1) | 90 (43.1) | 199 | (95.2) | 4 | (4.4) |

Larvae were released from the egg capsules during the late three-setiger stage, and they were able swimmers. Larvae were planktotrophic until they reached the 17-setiger stage, a process that required more than two months at 15 °C. The length of planktonic three-setiger larvae was 250-320 µm. The embryonic yolk was no longer present by the six-setiger stage. The 13-setiger larvae were about 750 µm long, and palps were present. Gastrotrochs were located on setigers 3, 5, 7 and 10. The 14- ( Fig. 4C) and 15-setiger larvae were about 800 and 950 µm long, respectively. A modified prostomium and yellow pigmentation were apparent. The 16- and 17-setiger larvae (Fig. 4D) were 1.0 and 1.25 mm long, respectively. Palps were elongated to the end of the fifth setiger and four eye spots were in trapezoidal arrangement. Distinct black pigmentation was present on the dorsal surface of the 15th, 16th and 17th setigers, and gastrotrochs were present on setigers 7, 10, 13 and 15. The modified spines and accompanying companion setae on setiger 5 developed and emerged at this stage; they were present on some worms at the 15-setiger stage. A caruncle gradually developed and appeared at the 14-setiger stage. The 17-setiger stage was reached in a minimum of 36 days and a maximum of 65 days.

The larvae of *P. variegata* were not easily induced to settle and metamorphose. Only five out of 200 larvae completed metamorphosis. These larvae took more than two months to settle and metamorphose after hatching. Almost all the 17-setiger larvae were alive for more than two months and up to as much as three months without settling and metamorphosing. There was no apparent change in morphology of these larvae apart from slight elongation.

## DISCUSSION

A large number of worms of the genus *Polydora* were found to have bored into the shells of sown cultured scallops in Abashiri Bay. The boring species were *P. variegata, P. websteri, P. concharum, P. concharum*

Source : MNHN, Paris

subspecies and *P. convexa*. The relative frequencies of these species were 55.5 %, 17.3 %, 0.4 %, 26.6 % and 0.2 %, respectively, throughout the year. We have studied the reproductive characteristics and settling periods of *P. websteri* and *P. concharum* subspecies.

FIG. 4. — Photographs of larvae of *Polydora variegata*. A, Early three-setiger larva; B, late three-setiger larvae; C, 14-setiger larva; D, 17-setiger larva.

There are two reproductive populations of *P. websteri* which are found in early summer and in autumn (SATO, 1988). Females apparently produce egg string only once with approximately 500 eggs per batch. Their juveniles tend to settle on the ventral edge of the left valve, in the same way as *P. variegata*, after approximately one month's planktonic life. Their life span seems to be one year.

No mature individuals were observed in the case of *P. concharum* ssp. The strong regenerative activity and the fact that more than two worms inhabit each burrow suggest that asexual reproduction might be occurring in this species. Five species of the genus *Polydora*, which coexist in the same scallop shell, seem to have different life-cycle patterns.

There are many reports with descriptions of the reproduction of the genus *Polydora* (WILSON,1928; HEMPEL, 1957; HATFIELD, 1965; MIZUMOTO, 1966; BLAKE, 1969; RASMUSSEN, 1973; DAY & BLAKE, 1979; ANGER, ANGER & HAGMEIER, 1986; RADASHEVSKII, 1986). For many species of *Polydora*, the life span has been reported to be about one year or less and they die after their first or several spawnings within a year (SÖDERSTROM, 1920; LAMBECK & VALENTIJN, 1987). Under natural conditions, only the example from northeast England offers the possibility of some worms surviving for more than a year and spawning again (GUDMUNDSSON, 1985). In the case of *P. variegata*, however, all the worms seem to survive for 2.5 years after having settled on the scallop shells. They spawn during the first year and also in the subsequent year, producing one to several batches of egg strings during the main spawning season. *P. variegata* produced 300 to 1,000 eggs per batch in the first year and 800 to 5,700 eggs in the second. Moreover, the 1-year-olds apparently produced egg strings year round. The

Source : MNHN, Paris

maximum body size of 30 mm in length and 1.6 mm in width, the high reproductive activity and a long life span are characteristic of the boring polychaete *P. variegata*.

The life history of *P. variegata* is shown schematically in figure 5.

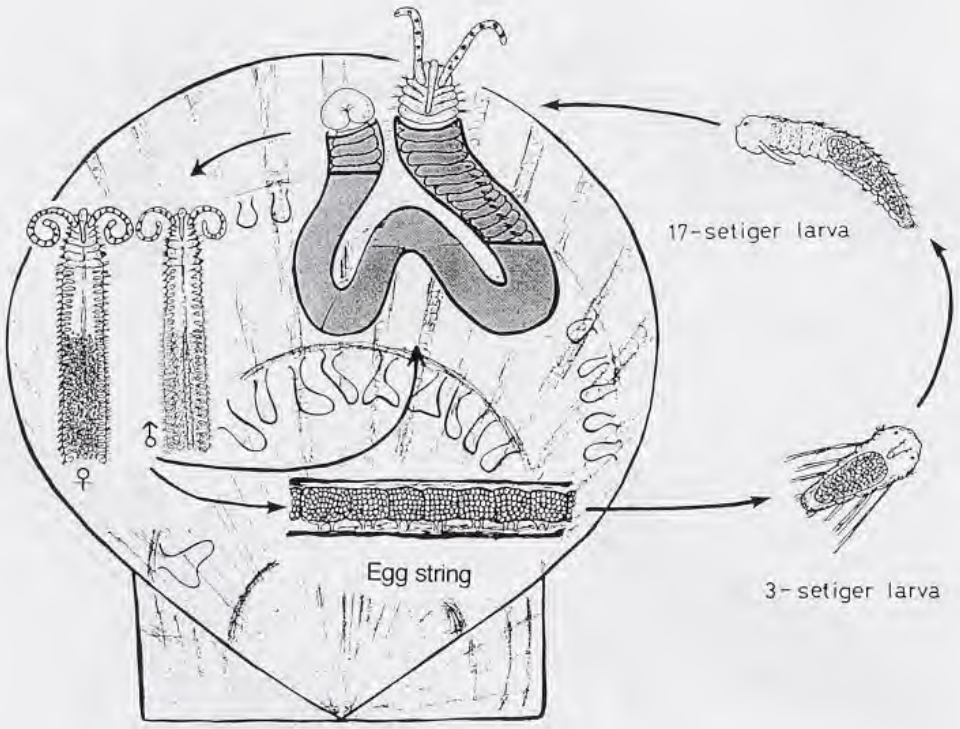



FIG. 5. — Schematic diagram showing life history of *Polydora variegata*.

Live *Polydora* worms were found only in the shells of live scallops or in shells just after the death of scallops. No worms were collected from the benthos. From a depth of 15 to 45 m in Abashiri Bay, *Tectonatica janthostomorides, Mercenaria stimpsoni, Fusitriton oregonensis, Glycymeris yessoensis, Chlamys swifti* and *Buccinum ochotence* live among high densities of natural and sown scallops. We have observed live *Polydora* species only in the shells of *T. janthostomoides* and *F. oregonensis*. Some worms of *P. websteri* were taken from the shells of *T. janthostomoides*, and many worms of *P. concharum* ssp. were extracted from those of *F. oregonensis*. *P. variegata* was never extracted from any of these species.

*P. variegata* and *P. websteri* settle on the ventral edge of the left valve. In contrast, *P. concharum* ssp. seems to have no tendency in settling region. However, its burrows are found in aggregates. In the case of *P. websteri* and *P. concharum*, each species was found in only a few shells into which no other species had bored. Very few worms of *P. variegata* were taken from these shells. The number of *Polydora* extracted from one shell fluctuated greatly which may be the result of patchy distribution of larvae.

The tendency of *P. variegata* to settle on the ventral edge of the left valve seems to suggest that (1) larvae are induced to settle by some chemical substance(s) contained in the newly formed periostracum, and (2) it is more advantageous to settle on this edge of the left valve for feeding. Indeed, *Polydora* worms are basically suspension feeders and the scallop always tends to face the oncoming water current.

Identification of the species in the genus *Polydora* has been somewhat confused in Japan. *P. variegata* was mistaken for *P. ciliata* until it was redescribed as a new species by IMAJIMA & SATO in 1984. The distribution of *P. variegata* has not yet been investigated. We have reported that *P. variegata* is distributed in the Okhotsk Sea, Mutsu Bay and along the Pacific coast of Tohoku district (MORI *et al.*, 1985; SATO-OKOSHI & NOMURA, 1990). Our present data indicate that *P. variegata* is distributed extensively in the northern part of Japan.

It would be advantageous to prevent the settlement of *P. variegata* on the shells of scallops during the first winter season after sowning, and it would seem better to harvest scallops after two years in Abashiri Bay. We

Source : MNHN, Paris

mentioned previously that when numerous worms settle on the ventral edge of the left valve of 1-year-old sown scallops in the first winter season after sowing, the site of attachment of the adductor muscle to the left valve overlaps the region of the shell that is heavily infested with 1-year-old worms because the adductor muscle inceases in size and shifts its position toward the ventral side during growth in the following year (MORI *et al.*, 1985; SATO-OKOSHI *et al.*, 1990). Scallops that are heavily infested with *Polydora* at the site of attachment of the adductor muscle may be weakened and penetration at this site may be fatal (MORI *et al.*, 1985). Furthermore, worms become a year old before harvesting the scallops when they settle on scallop shells during the first winter season, and the 1-yr-old worms produce many offsprings.

It would be of importance to determine the length of the planktonic period and the mechanism of settling of the worm, as well as to determine why the larvae prefer to settle on the ventral edge of the left valve rather than the right valve of the scallop. Experimentation in the laboratory may help to clarify these issues.

## ACKNOWLEDGEMENTS

We are indebted to Prof. Tadashi NOMURA of the Department of Fishery Science, Faculty of Agriculture, Tohoku University, for making it possible for us to carry out this study. Thanks are also due to the staff of the Abashiri Scallop Research Laboratory, Abashiri, for their assistance in collecting the materials, and to Dr. Kenji OKOSHI of the Department of Biotechnology, Senshu University of Ishinomaki, for his critical comments on the manuscript.

## REFERENCES

ANGER, K., ANGER, V. & HAGMEIER, E., 1986. — Laboratory studies on larval growth of *Polydora ligni*, *Polydora ciliata* and *Pigospio elegans* Polychaeta Spionidae. *Helgolander Meeresunters*, **40** : 377-396.

BLAKE, J.A., 1969. — Reproduction and larval development of *Polydora* from northern New-England (Polychaeta; Spionidae). *Ophelia*, **7** : 1-63.

BLAKE, J.A. & EVANS, J.W., 1972. — *Polydora* and related genera as borers in mollusk shells and other calcareous substrates (Polychaeta; Spionidae). *Veliger*, **15** : 235-249.

DARO, M.H. & POLK, P., 1973. — The autoecology of *Polydora ciliata* along the Belgian coast. *Neth. J. Sea Res.*, **6** : 130-140.

DAY, R.L. & BLAKE, J.A., 1979. — Reproduction and larval development of *Polydora giardi* Mesnil (Polychaeta; Spionidae). *Biol. Bull. mar. biol. Lab., Woods Hole*, **156** : 20-30.

DORSETT, D.A., 1961. — The reproduction and maintenance of *Polydora ciliata* (Johnst.) at Whitstable. *J. mar. biol. Ass. U.K.*, **41** : 383-396.

GUDMUNDSSON, H., 1985. — Life history patterns of polychaete species of the family Spionidae. *J. mar. biol. Ass. U.K.*, **65** : 93-111.

HATFIELD, P.A., 1965. — *Polydora commensalis* Andrews Larval development and observations on adults. *Biol. Bull. mar. biol. Lab., Woods Hole*, **128** : 356-368.

HEMPEL, C., 1957. — Über den Röhrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta Sedentaria) der Deutschen küsten. *Helgoländer wiss. Meeresunters*, **6** : 100-135.

IMAJIMA, M. & SATO, W., 1984. — A new species of *Polydora* (Polychaeta, Spionidae) collected from Abashiri Bay, Hokkaido. *Bull. Natn. Sci. Mus., Tokyo (Ser. A)*, **10** : 57-62.

LAMBECK, R.H.D. & VALENTIJN, P., 1987. — Distribution dynamics and productivity of a colonizing *Polydora quadrilobata* and an established *Polydora ligni* polydorid polychaete in Lake Grevelingen, an enclosed estuary in the southwest Netherlands. *Neth. J. Sea Res.*, **21** : 143-158.

MIZUMOTO, S., 1966. — Studies on the disease of the shells of pearl oyster (*Pinctada martensii*). 2. On the seasonal variation in occurrence *Polydora ciliata* in shells of pearl oyster. *Bull. natl. Pearl Res. Lab.*, **11** : 1368-1377.

Source : MNHN, Paris

MORI, K., SATO, W., NOMURA, T. & IMAJIMA, M., 1985. — Infestation of the Japanese scallop *Patinopecten yessoensis* by the boring polychaetes, *Polydora*, on the Okhotsk Sea coast of Hokkaido, especially in Abashiri waters. *Bull. Jap. Soc. Scient. Fish.*, **51** : 371-380.

RADASHEVSKII, V.I., 1986. — Reproduction and larval development of the polychaete *Polydora ciliata* in Peter the Great Bay of the Sea of Japan Russian SFSR USSR. *Biol. Morya, Vladivost*, **6** : 36-43.

RASSMUSSEN, E., 1973. — Systematics and ecology of the Isefjord marine fauna. *Ophelia*, **11** : 1-495

SATO, W., 1988. — *Species, life history and infestation of the boring polychaetes, in the genus Polydora, in Japan.* Dissertation, Tohoku University, Sendai, Japan, 115 pp.

SATO-OKOSHI, W., SUGAWARA, Y. & NOMURA, T., 1990. — Reproduction of the boring polychaete *Polydora variegata* inhabiting scallops in Abashiri Bay, North Japan. *Mar. Biol.*, **104** : 61-66.

SATO-OKOSHI, W. & NOMURA, T., 1990. — Infestation of the Japanese scallop *Patinopecten yessoensis* by the boring polychaetes *Polydora* on the coast of Hokkaido and Tohoku District. *Nippon Suisan Gakkaishi*, **56** (10): 1593-1598.

SATO-OKOSHI, W. & OKOSHI, K., 1992. — *Polydora*-Scallop Interactions: Structural defenses in resistance to burrowing. *Aquabiology*, **14** : 113-119.

SÖDERSTRÖM, A., 1920. — *Studien über die Polychaetenfamilie Spionidae*. Inaugur. Dissert. University Uppsala, 286 pp.

WILSON, D.P., 1928. — The larvae of *Polydora ciliata* Johnston and *Polydora hoplura* Claparède. *J. mar. biol. Ass. U.K.*, **15** : 567-596.

ZAJAC, R.N., 1992. — Population ecology of *Polydora ligni* (Polychaeta: Spionidae). 1. Seasonal variation in population characteristics and reproductive activity. *Mar. Ecol. Prog. Ser.*, **77** : 197-206.

Source : MNHN, Paris

# Annelid polychaete populations of the Order Eunicida from the southern Gulf of Mexico

*Vivianne SOLIS-WEISS, Luz Verónica RODRIGUEZ-VILLANUEVA, Alejandro GRANADOS-BARBA, Victor OCHOA-RIVERA Luis MIRANDA-VAZQUEZ & Pablo HERNANDEZ-ALCANTARA*

Instituto de Ciencias del Mar y Limnología, UNAM
Apdo. Postal 70-305, México, D.F.04510, México

ABSTRACT

The Polychaete populations of the Order Eunicida, in the Mexican section of the Gulf of Mexico were analyzed. Seventy six stations on soft bottoms were sampled from the continental shelf region (15 to 200 m) from Tampico to Progreso covering approximately 46,000 km$^2$. Sediments varied from fine muds to mixed sediments in the "terrigen" western zone to calcareous sands and coralline fragments in the eastern "carbonated" zone. A total of 3,135 organisms were identified. Among the five families present, 54 species were distributed as follows: Onuphidae: 17 (920 individuals), Lumbrineridae: 16 (1808), Eunicidae: 14 (326), Arabellidae: 4 (76), Dorvilleidae: 3 (5). Four zones were identified. The dominant species in zone 1 was *Lumbrineris coccinea*, in zone 2: *L. latreilli* and in zones 3 and 4: *S. verrilli*. Sediment composition and depth were the major factors in the distribution of the polychaetes. The greatest diversity of this group occured in shallow seas with calcareous sands.

RÉSUMÉ

**Les populations d'Annélides Polychètes de l'Ordre des Eunicida de la région méridionale du golfe du Mexique**

Les populations de Polychètes de l'Ordre des Eunicida du Golfe du Mexique ont été analysées. Soixante seize stations, sur fond meuble ont été retenues sur la plateforme continentale (de 15 à 200 m) de Tampico à Progreso dans une zone couvrant environ 46 000 km$^2$. Les sédiments varient depuis les vases fines jusqu'aux sédiments hétérogènes dans la zone occidentale "terrigène". Dans la zone orientale "carbonatée", les sédiments sont constitués de sables grossiers calcaires et de fragments de coraux. Au total, 3135 Polychètes furent dénombrés. Parmi les cinq familles présentes, 54 espèces furent identifiées : Onuphidae : 17 (920 individus), Lumbrineridae : 16 (1808), Eunicidae : 14 (326), Arabellidae : 4 (76), Dorvilleidae : 3 (5). Quatre zones ont été identifiées. L'espèce dominante dans la zone 1 est *Lumbrineris coccinea*, dans la

SOLIS-WEISS, V., RODRIGUEZ-VILLANUEVA, L.V., GRANADOS-BARBA, A. OCHOA-RIVERA, V., MIRANDA-VAZQUEZ, L. & P. HERNANDEZ-ALCANTARA, 1994.— Annelid Polychaete Populations of the Order Eunicida from the Southern Gulf of Mexico *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 559-566. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

zone 2 : *L. latreilli* et dans les zones 3 et 4 : *S. verrilli*. La composition sédimentaire et la profondeur sont les facteurs prépondérants expliquant la distribution des Polychètes de cet Ordre, les sables calcaires et les eaux peu profondes leur fournissant les conditions les plus favorables.

## INTRODUCTION

The polychaete fauna of the continental shelf in the U. S. region of the Gulf of Mexico is reasonably well documented. The checklist of species and complete list of references include PERKINS & SAVAGE (1975) and the recently published updated checklist by SALAZAR-VALLEJO (1992). The taxonomic guide to the polychaetes of the northern region of the Gulf by UEBELACKER & JOHNSON (1984) is the most modern and comprehensive work for the area. FAUCHALD's (1992) recent worldwide review of the genus *Eunice* was also a useful reference for this study. However, it is clear from these publications that most of the work has been done outside the Mexican

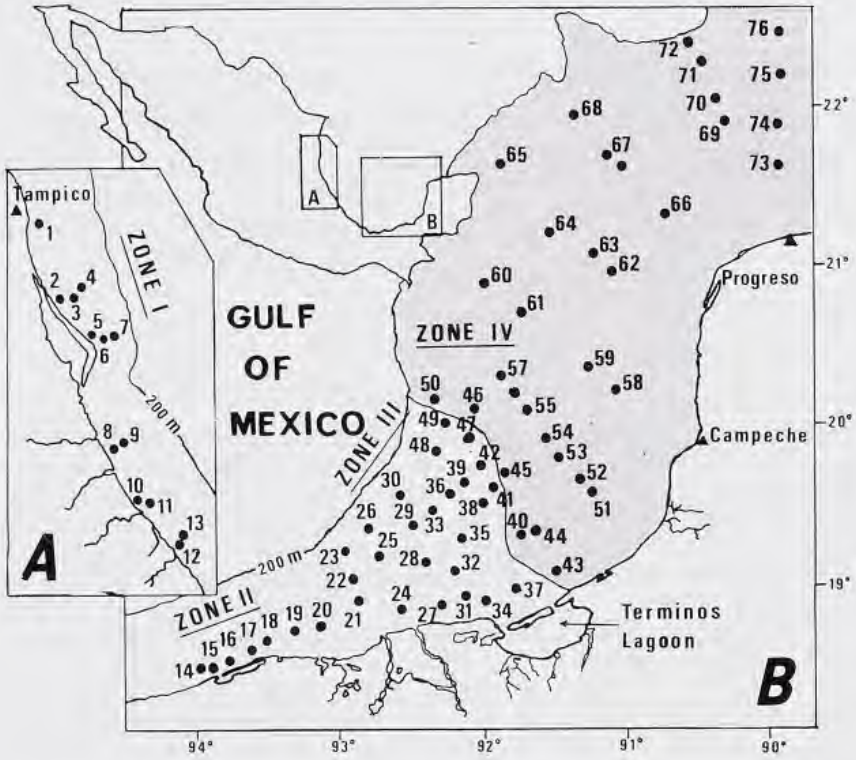



FIG. 1. — Study area: Southern Gulf of Mexico. Shading indicates the extent of the carbonated zone.

region of the Gulf. Information on this region is relatively scarce, especially from the continental shelf since RIOJA (1961, 1962), HARTMAN (1951), SOLIS-WEISS & CARREÑO (1986) IBAÑEZ-AGUIRRE & SOLIS-WEISS (1986); previous studies concentrated on sampling beach areas or coastal lagoons (RIOJA, 1946a, 1946b, 1958, 1959, MENDEZ-UBACH, SOLIS–WEISS & CARRANZA–EDWARDS, 1986; SALAZAR-VALLEJO *et al.*, 1989; HERNANDEZ-ALCANTARA & SOLIS-WEISS, 1991).

The first extensive sampling of the continental shelf of the Mexican Gulf region was initiated by our group in 1987 thanks to the acquisition, a few years earlier, of the R/V "Justo Sierra". Several cruises were undertaken, especially in the South Western area of the Gulf. As expected, the polychaete fauna collected was very abundant and diverse. The best represented polychaetes there were those of the order Eunicida, both in terms of diversity and abundance (SOLIS-WEISS *et al.*, 1991, GRANADOS-BARBA & SOLIS-WEISS, 1994).

Source : MNHN, Paris

The purpose of this paper is to analyze those populations in their structure and distribution, and to determine the influence of the environmental factors on the distribution of this order of polychaetes.

## STUDY AREA

The continental shelf of the Gulf of Mexico from Tampico to Progreso is an extensive area between longitudes 90°23' and 97°45' and latitudes 18°20' to 22°31'. The influence of the discharge from rivers to the sea occurs only in the northern and central regions. This terrigen zone (YAÑES-CORREA, 1971) is characterized by mixed or muddy sediments while to the east, biogenic or carbonated calcareous sands and coral reef rubble are the main components of the sediment (Fig. 1). The area is shallow (up to about 50–60 m) with several small coralline islands dotting the outer continental shelf.

The environment is influenced, in the terrigen zone, by the intensive off-shore activity of the oil well drilling and production where the majority of the oil fields of Mexico are found. This area also supports a rich fishery and the most productive area for shrimps in Mexico.

The principal current flow comes from the North East (Yucatán peninsula) and follows the shore to the north with some reversal in the winter (VIDAL *et al.*, 1990).

## MATERIALS AND METHODS

Sampling was done on board the R/V "Justo Sierra" as part of the interdisciplinary institutional projects "Determinación del impacto ambiental provocado por las actividades de extracción petrolera en la Sonda de Campeche a través de estudios biológicos, geoquímicos y sedimentológicos (IMCA), and "Dinámica oceánica y su relación con el deterioro ambiental en la porcion sur del Golfo de México" (DINAMO) (SOLIS-WEISS *et al.*, 1991). The area was divided into four zones according to latitude and type of sediment predominantly present (Figs. 1 & 2). Zones 1 (stations 1–13) and 2 (stations 14–20) are characterized by a narrow shelf, mixed sediments and river discharge, but the two zones are oriented differently and latitudinally apart sufficiently so that the hydrologic conditions are different. Zone 3 (stations 21–50) presents a widening continental shelf where oil platforms are present. Zone 4 (stations 51–76) begins at the limit of the terrigen and the carbonated zones. The shelf edge is close to its maximum extension (245 Km), the influence of river run–off is non existent and the sediments tend to be coarser and coralline in nature.

Transects were taken along the continental shelf at depths ranging from 15 to 200 m. and covered an approximate area of 46,000 km$^2$. Seventy six stations were selected for this study (Fig. 1).

The fauna was collected with a 0.1 m$^2$ (10 l) Smith McIntyre grab. Three cruises are considered herein (IMCA II (September 19-29,1988), IMCA IV (September 25-October 8, 1989) and DINAMO II (October 25-November 8, 1990).

The samples were sieved through a 0.5 mm screen, fixed with formalin (10 %), then sorted and preserved with alcohol (70 %) following the methodology of FAUCHALD (1977). A solution of methylene blue was routinely used for assistance in identification.

Density is defined as the number of individuals per 0.1 m$^2$.

Frequency is expressed as the percentage of occasions in which the species was present in the stations of each zone. Species richness is the number of species present per station. Diversity indexes were calculated for the four zones. The SHANNON-WIENER index was calculated as well as the Evenness index following PIELOU (1977), and the SIMPSON index (ODUM, 1971). These results are shown in Figure 3.

## RESULTS AND DISCUSSION

The Eunicida were represented by 3,135 individuals, grouped into five families, 18 genera and 54 species (Table 1). There were two new records for Mexico : *Lumbrineris heteropoda* and *L. paradoxa*, and about seven new species which are now under study.

The five families were distributed as follows: the Onuphidae accounted for 17 species and 920 organisms, the Lumbrineridae 16 species and 1808 organisms, the Eunicidae 14 species and 326 organisms, the Arabellidae 4 species and 76 organisms and the Dorvilleidae 3 species and 5 organisms.

Source : MNHN, Paris

TABLE 1. — Frequency (FREQ.) and Mean Density (DE) values for the species of Eunicida found in the study area.

| SPECIES | ZONE 1 | | ZONE 2 | | ZONE 3 | | ZONE 4 | |
|---|---|---|---|---|---|---|---|---|
| | FREQ. | DE | FREQ. | DE | FREQ. | DE | FREQ. | DE |
| *Diopatra cuprea* (Bosc, 1802) | 38,46 | 0,14 | 42,86 | 0,19 | 33,33 | 0,47 | 38,46 | 0,45 |
| *Diopatra neotridens* Hartman, 1944 | 15,38 | 0,09 | 14,29 | 0,06 | 16,67 | 0,06 | 7,69 | 0,03 |
| *Diopatra papillata* Fauchald, 1968 | 7,69 | 0,02 | | 0,00 | | 0,00 | 11,54 | 0,07 |
| *Diopatra tridentata* (Hartman, 1944) | 61,54 | 0,24 | 14,29 | 0,08 | 13,33 | 0,04 | 15,38 | 0,07 |
| *Hyalinoecia juvenalis* (Moore, 1911) | | 0,00 | 14,19 | 0,02 | | 0,00 | 3,85 | 0,01 |
| *Hyalinoecia tubicola* (Müller, 1776) | 15,38 | 0,03 | | 0,00 | | 0,00 | | 0,00 |
| *Kinbergonuphis pigmentata* (Fauchald, 1968) | | 0,00 | | 0,00 | | 0,00 | 7,69 | 0,03 |
| *Kinbergonuphis abyssalis* (Fauchald, 1968) | | 0,00 | | 0,00 | | 0,00 | 3,85 | 0,01 |
| *Kinbergonuphis orensanzi* (Fauchald,1982) | 46,15 | 0,23 | 42,86 | 0,52 | 40,00 | 0,49 | 61,54 | 1,37 |
| *Kinbergonuphis pulchra* (Fauchald, 1980) | 15,38 | 0,09 | | 0,00 | | 0,00 | 15,38 | 0,10 |
| *Kinbergonuphis simoni* (Santos, Day & Rice, 1981) | | 0,00 | 57,14 | 0,30 | | 0,00 | 34,62 | 0,58 |
| *Mooreonuphis stigmatis* (Treadwell, 1922) | | 0,00 | | 0,00 | | 0,00 | 11,54 | 0,06 |
| *Mooreonuphis dangrigae* (Fauchald, 1980) | | 0,00 | 14,29 | 0,07 | | 0,00 | 19,23 | 0,09 |
| *Mooreonuphis nebulosa* (Moore, 1911) | 7,69 | 0,02 | | 0,00 | | 0,00 | 15,38 | 0,12 |
| *Mooreonuphis sp.* 1 | | 0,00 | | 0,00 | | 0,00 | 7,69 | 0,43 |
| *Mooreonuphis sp.* 2 | | 0,00 | | 0,00 | 3,33 | 0,08 | | 0,00 |
| *Paradiopatra hartmanae* (Kirkegaard, 1980) | 7,69 | 0,06 | | 0,00 | 10,00 | 0,07 | 7,69 | 0,04 |
| *Eunice afra* Peters, 1854 | | 0,00 | | 0,00 | | 0,00 | 3,85 | 0,01 |
| *Eunice antennata* (Savigny, 1818) | | 0,00 | | 0,00 | | 0,00 | 3,85 | 0,01 |
| *Eunice cariboea* Grube, 1856 | 7,69 | 0,04 | | 0,00 | | 0,00 | 7,69 | 0,01 |
| *Eunice filamentosa* Grube, 1856 | 7,69 | 0,02 | | 0,00 | | 0,00 | 3,85 | 0,06 |
| *Eunice sp.* 1 | 7,69 | 0,02 | | 0,00 | 3,33 | 0,01 | 3,85 | 0,01 |
| *Eunice sp.* 2 | | 0,00 | | 0,00 | | 0,00 | 3,85 | 0,12 |
| *Eunice vittata* (Delle Chiaje, 1828) | 7,69 | 0,02 | 42,86 | 0,53 | 3,33 | 0,01 | 50,00 | 0,80 |
| *Eunice websteri* Fauchald, 1969 | 7,69 | 0,02 | | 0,00 | | 0,00 | 11,54 | 0,08 |
| *Lysidice ninetta* Audouin & Milne Edwards, 1833 | | 0,00 | | 0,00 | | 0,00 | 26,92 | 0,26 |
| *Marphysa bellii* (Audouin & Milne Edwards, 1834) | 46,15 | 0,13 | | 0,00 | 10,00 | 0,02 | 11,54 | 0,02 |
| *Marphysa disjunta* Hartman, 1961 | 15,38 | 0,06 | | 0,00 | 3,33 | 0,01 | | 0,00 |
| *Marphysa* ca. *posterobranchia* Day, 1962 | | 0,00 | | 0,00 | 3,33 | 0,01 | 3,85 | 0,02 |
| *Marphysa sp.* 1 | 7,69 | 0,03 | | 0,00 | | 0,00 | 3,85 | 0,02 |
| *Nematonereis hebes* Verrill, 1900 | 7,69 | 0,02 | | 0,00 | 6,67 | 0,01 | 38,46 | 0,22 |
| *Lumbrinerides acuta* (Verrill, 1875) | | 0,00 | | 0,00 | | 0,00 | 11,54 | 0,10 |
| *Lumbrinerides dayi* Perkins 1979 | | 0,00 | 57,14 | 0,76 | | 0,00 | | 0,00 |
| *Lumbrineriopsis paradoxa* (Saint Joseph, 1888) | | 0,00 | | 0,00 | | 0,00 | 15,28 | 0,04 |
| *Paraninoe brevipes* (McIntosh, 1903) | | 0,00 | | 0,00 | 3,33 | 0,01 | | 0,00 |
| *Lumbrineris coccinea* (Renier, 1804) | 53,85 | 0,54 | 71,43 | 0,55 | 16,67 | 0,07 | 34,62 | 0,27 |
| *Scoletoma ernesti* Perkins, 1979 | 53,85 | 0,44 | 14,29 | 0,06 | 13,33 | 0,07 | 42,31 | 0,37 |
| *Lumbrineris heteropoda* Marenzeller, 1879 | | 0,00 | | 0,00 | 3,33 | 0,02 | | 0,00 |
| *Lumbrineris inflata* Moore, 1911 | | 0,00 | | 0,00 | | 0,00 | 3,85 | 0,01 |
| *Lumbricalus dayi* Frame 1992 | 23,08 | 0,07 | 28,57 | 0,09 | 3,33 | 0,01 | 11,54 | 0,04 |
| *Lumbrineris latreilli* (Aud. & Milne Edw., 1834) | 30,77 | 0,17 | 85,71 | 1,75 | 13,33 | 0,08 | 50,00 | 0,40 |
| *Lumbrineris sp.* 1 | | 0,00 | | 0,00 | 6,67 | 0,02 | | 0,00 |
| *Lumbrineris sp.* 2 | | 0,00 | 28,57 | 0,64 | 3,33 | 0,01 | | 0,00 |
| *Scoletoma tenuis* (Verrill, 1873) | 38,46 | 0,26 | 71,43 | 0,57 | 46,67 | 0,42 | 46,15 | 1,85 |
| *Scoletoma verrilli* Perkins, 1979 | 46,15 | 0,43 | 42,86 | 0,15 | 33,33 | 0,71 | 76,92 | 4,13 |
| *Ninoe brasiliensis* Kinberg, 1865 | | 0,00 | 14,29 | 0,04 | 10,00 | 0,05 | | 0,00 |
| *Ninoe leptognatha* Ehlers, 1900 | 38,46 | 0,25 | | 0,00 | 50,00 | 0,21 | 38,46 | 0,71 |
| *Arabella iricolor* (Montagu, 1804) | 7,69 | 0,02 | 14,29 | 0,02 | | 0,00 | 3,85 | 0,04 |
| *Arabella multidentata* (Ehlers, 1887) | 7,69 | 0,02 | 14,29 | 0,04 | | 0,00 | 38,46 | 0,11 |
| *Drilonereis longa* Webster, 1879 | | | | 0,00 | 10,00 | 0,02 | 23,08 | 0,06 |
| *Drilonereis spatula* (Treadwell, 1911) | | | 42,86 | 0,10 | | | | 0,00 |
| *Dorvillea* ca. *sociabilis* (Webster, 1879) | | | | 0,00 | | | 3,85 | 0,02 |
| *Protodorvillea kefersteini* (McIntosh, 1869) | | | 28,57 | 0,24 | | | | 0,00 |
| *Schistomeringos pectinata* Perkins, 1979 | | | | | | | 3,85 | 0,01 |

The dominant family in terms of abundance was the Lumbrineridae although there were different dominant species with the latitude (see below).

The distribution of the five families present in the study area is shown in Table 2. The lumbrinerids accounted for more than 55 % of the organisms in the order in all zones and up to around 70 % in zone 2. The dorvilleids were poorly represented (3.49 % in zone 2; 0.20 in zone 4, none in zones 1 and 3). The onuphids accounted for

Source : MNHN, Paris

about 1/4 of the population in each zone, and were best represented in zone 3 (40.94 %). The eunicids varied from 2.6 % in zone 3 to 12.45 % in zone 4.

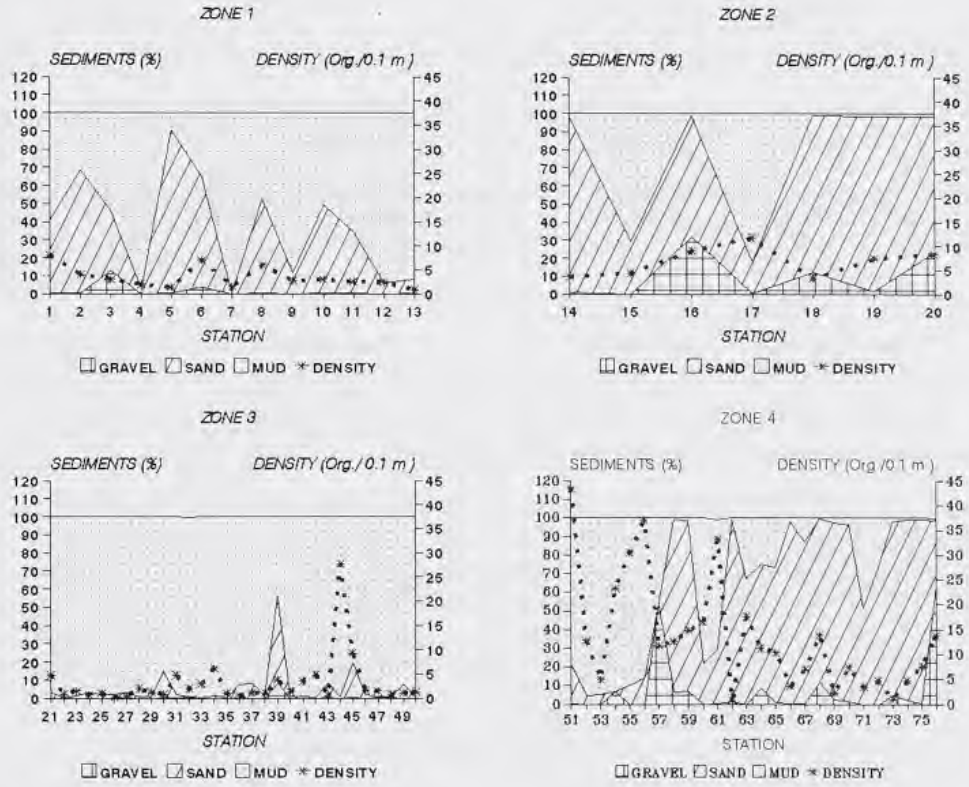



FIG. 2. — Sediment composition and density of the populations of Eunicea in the study area.

The highest diversity and density occured in zone 4. As seen in Table 2, mean densities were significantly higher from zone 4 for each family, except for the dorvilleids which are very poorly represented from all zones (Table 2). Zone 4 is characterized by shallow waters and coarse biogenic sediments (Fig. 2). In the other zones, the highest densities were also found in shallow waters in mixed or coarse sediments (Fig. 2). Densities decreased with increasing depth.

The highest diversity or species richness was found in zone 4 (43 species). Around eight species per station were found, compared to an average of three species per station at zones 1–3. Diversity values were higher in zones 1, 2 and
4 (Fig. 3). However, higher variations in those values were noted in zone 1. Again, there was a tendency for lower values as depth increased in all zones with less contrast in zone 4 (Fig. 3). Evenness and dominance values varied more in zones 3 and 4.

The distribution patterns were directly related to the dominance of some species analyzed below.

In zone 1 (Table 2), 10 species were found to be both abundant and frequent: *Lumbrineris coccinea, L. ernesti, L. verrilli, S. tenuis, L. latreilli, Ninoe leptognatha, Diopatra tridentata, D. cuprea, Kinbergonuphis orensanzi* and *Marphysa bellii*. The dominant species were: *L. coccinea L. ernesti* and *S. verrilli*.

Among the frequent species in zone 2 (Table 2), only one had a density value larger than 1: *L. latreilli*, and six were found with values greater than 0.5: *Lumbrinerides dayi, Kinbergonuphis orensanzi, Eunice vittata, S. tenuis,*

Source : MNHN, Paris

*L. coccinea*, *L. sp. 2*. The dominant species were: *L. latreilli*, *L. tenuis*, *L. coccinea* and *Lumbrinerides dayi* in zone 2.

Four species in zone 3, which combine high densities with high frequency values can be considered dominant: *S. verrilli*, *K. orensanzi*, *Diopatra cuprea* and *S. tenuis* (Table 3).

Species richness was highest in zone 4, where 10 species combined high densities with high frequencies: *S. verrilli*, *S. tenuis*, *K. orensanzi*, *E. vittata*, *N. leptognatha*, *K. simoni*, *D. cuprea*, *Mooreonuphis sp. 1*, *L. latreilli* and *L. ernesti* (Table 3). The dominant species were: *S. verrilli*, *S. tenuis* and *K. orensanzi*.

TABLE 2. — Mean Densities (ind. 0.1 $m^{-2}$) of individual families and percentage (%) of the total populations of Eunicida found in the study area.

| | Onuphidae | | Eunicidae | | Lumbrineridae | | Arabellidae | | Dorvilleidae | |
|---|---|---|---|---|---|---|---|---|---|---|
| | mean density | % | mean density | % | mean density | % | mean density | % | mean density | % |
| ZONE 1 | 0.92 | 26.79 | 0.34 | 9.86 | 2.15 | 62.37 | 0.03 | 0.98 | 0.00 | 0.00 |
| ZONE 2 | 1.24 | 18.74 | 0.53 | 7.92 | 4.62 | 69.59 | 0.01 | 0.15 | 0.24 | 3.59 |
| ZONE 3 | 1.21 | 40.53 | 0.08 | 2.63 | 1.67 | 56.04 | 0.02 | 0.78 | 0.00 | 0.00 |
| ZONE 4 | 3.45 | 26.03 | 1.65 | 12.45 | 7.92 | 59.76 | 0.21 | 1.56 | 0.03 | 0.20 |

As can be seen, the lumbrinerids were dominant but the dominant species varied with the latitude. Henceforth, in zone 1 it was *L. coccinea* (15.81 % of the population) and *S. ernesti* (13 %) followed by *S. verrilli* (12.7 %). Together they represented 41.51% of the total population in that zone. In zone 2, *L. latreilli* was the best represented (25.79 % of the population) followed by *Scoletoma tenuis* (8.48 %) and *L. coccinea* (8.08 %) representing 47.45 % of the population. In zone 3, *S. verrilli* (23.62 %) dominated followed by *S. tenuis* (13.94 %) and *K. orensanzi* (16.26 %) to total 53.82 %. In zone 4: *S. verrilli* (30.63 %) *S. tenuis* (13.75 %) and *K. orensanzi* (10.17 %), to total 54.55 %. The most abundant and widely distributed species for the study area was *S. verrilli*, however it was not the dominant species in all samples.

*Scoletoma verrilli* is a species originally described from Florida by PERKINS (1979). It had been previously reported from very shallow depths (3-11 m) in sandy and coarse calcareous sands. It is widely distributed in the northern Gulf of Mexico at depths from 10 to 189 m from coarse sands to silty clays (UEBELACKER & JOHNSON, 1984).

Correlations with the distribution of these organisms with the parameters studied indicated the strongest relations with the type of sediment and depth. The sediments encountered (Fig. 2) were mixed with a tendency towards small grain sizes in zone 1. Zone 2 was mostly sandy. Zone 3 was predominantly muddy with some sand at stations 30, 36, 37, 39, 43, 45 and 49. Zone 4, in contrast, consisted of coarse, sandy sediments, which were derived from organic matter. Muddy sediments became a smaller fraction towards the East and Northeast as the influence of rivers discharge became non existent.

## CONCLUSIONS

The Eunicea from the soft bottoms of the continental shelf of the Gulf of Mexico consisted of five families, 18 genera and 54 species. The lumbrinerids were the dominant family in terms of abundance whereas the onuphids ranked higher in diversity with 17 species compared to 16 for the former. The dominant species varied according to latitude with *Lumbrineris coccinea* in zone 1, *L. latreilli* in zone 2 and *S. verrilli* in zones 3 and 4. *Scoletoma verrilli* was the most characteristic species in terms of abundance and distribution throughout the area.

## ACKNOWLEDGEMENTS

We would like to thank especially DGAPA-UNAM (project DINAMO IN209789) for its financial support at all stages of this project. Thanks are also due to the members of the Sedimentology and Marine Chemistry Labs of

Source : MNHN, Paris

the ICML-UNAM for their help in the environmental data and to all participants in the IMCA and DINAMO oceanographic cruises.

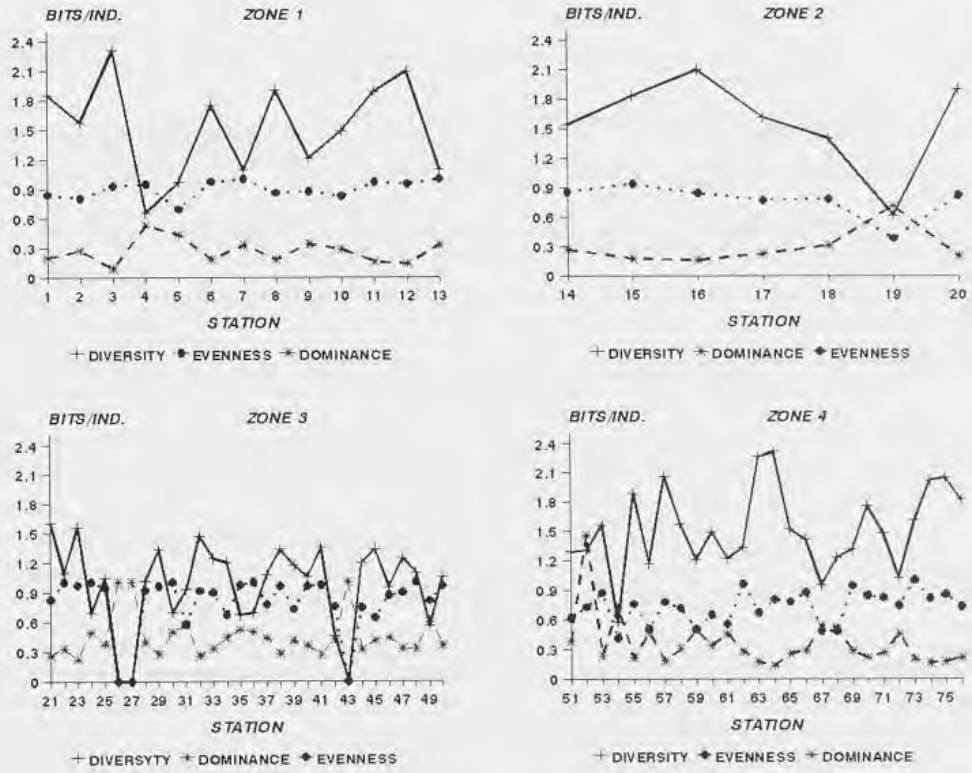



FIG. 3. — Diversity, Dominance and Evenness values recorded for the populations of Eunicea in the study area.

## REFERENCES

FAUCHALD, K., 1977. — The Polychaete Worms. Definitions and keys to the orders, families and genera. *Nat. Hist. Mus. of Los Angeles County, Sci. Ser.*, **28** : 1-190.

FAUCHALD, K., 1992. — A review of the Genus *Eunice* (Polychaeta: Eunicidae) Based upon Type Material. *Smithsonian Contr. to Zool.*, **523** : 422.

GRANADOS-BARBA A. & SOLIS-WEISS, V., 1994. — New records of Polychaetous Annelids (Order: Eunicida) from the Southeastern Gulf of Mexico. *Bull. Mar. Sci.*, **54** : 420-427.

HARTMAN, O., 1951. — The littoral Marine Annelids of the Gulf of Mexico. *Pub. Texas Univ. Inst. Mar. Sci.*, **2** : 7-124.

HERNANDEZ-ALCANTARA, P. & SOLIS-WEISS, V., 1991. — Ecological aspects of the polychaetous populations associated with the red mangrove *Rhizophora mangle* at the Laguna de Términos, southern part of the Gulf of Mexico. *Ophelia* Suppl., **5** : 451-462.

IBAÑEZ-AGUIRRE, A. L. & SOLIS-WEISS, V., 1986. — Anélidos poliquetos de las praderas de *Thalassia testudinum* del noroeste de la Laguna de Términos, Campeche. *Rev. Biol. Trop.*, **1** : 35-47

MENDEZ-UBACH, M. N., SOLIS-WEISS, V. & CARRANZA-EDWARDS, A., 1986. — La importancia de la granulometría en la distribución de organismos bentónicos. Estudio de playas del estado de Veracruz, México. *An. Inst. Cienc. del Mar y Limnol., Univ. Nal. Autón. México*, **13** : 45-56.

ODUM, E. P., 1971. — *Fundamentals of Ecology*, 3d. Edition Saunders, Philadelphia, 574 pp

Source : MNHN, Paris

PERKINS, T. H. & SAVAGE, T., 1975. — A bibliography and checklist of polychaetous annelids of Florida, the Gulf of Mexico, and the Caribbean Region. *Florida Mar. Res. Pub.*, **14** : 1-62.

PIELOU, E. C., 1977. — *Mathematical Ecology*. Wiley Interscience, New York, 384 pp.

RIOJA, E., 1946a. — Estudios Anelidológicos XIV. Observaciones sobre algunos poliquetos de las costas del Golfo de México. *An.Inst. Biol., Univ. Nal. Autón. México*, **17** : 193- 203.

RIOJA, E., 1946b. — Estudios Anelidológicos XV. Nereidos de agua salobre de los esteros del litoral del Golfo de México. *An. Inst. Biol., Univ. Nal. Autón. México*, **17** : 205-214.

RIOJA, E., 1958. — Estudios Anelidológicos XXI. Observaciones acerca de algunas especies de serpuidos de los géneros *Hydroides* y *Eupomatus* de las costas mexicanas del Golfo de México. *An. Inst. Biol., Univ. Nal. Autón. México*. **28** : 247-266.

RIOJA, E., 1959. — Estudios Anelidológicos XXII. Datos para el conocimiento de la fauna de anélidos poliquetos de las costas orientales de México. *An. Inst. Biol., Univ. Nal. Autón.México*, **29** : 219-301.

RIOJA, E., 1961. — Estudios Anelidológicos XXIV. Adiciones a la fauna de anélidos poliquetos de las costas orientales de México. *An. Inst. Biol., Univ. Nal. Autón. México*, **31** : 289-316.

RIOJA, E., 1962. — Estudios Anelidológicos XXV. Un nuevo género de la familia Pareulepidae (= Eulepethidae), del Golfo de México. *An. Inst. Biol., Univ. Nal. Autón. México*, **32** : 235-249.

SALAZAR-VALLEJO, S. I., DE LEON GONZALEZ, J. A. & H. SALAICES-POLANCO, 1989. — *Poliquetos (Annelida: Polychaeta) de Mexico: Generalidades, Claves ilustradas para familias y géneros, y Bibliografia-Lista de especies*. Libros Univ. Auton. Baja Calif. Sur, La Paz, 212 pp.

SALAZAR-VALLEJO, S., 1992. — Updated checklist of Polychaetes (Polychaeta) from the Gulf of Mexico, the Caribbean Sea and adjacent areas in the Western Atlantic Ocean. *In*: NAVARRO, D. & E. SUAREZ M (eds), *Diversidad Biológia en la Reserva de la Biosfera de Sian Ka'an Quintana Roo, México*. Vol. II. CIQRO/SEDESOL: 43-76.

SOLIS-WEISS, V. & CARREÑO, S., 1986. — Estudio prospectivo de la macrofauna béntica asociada a las praderas de *Thalassia testudinum* en la Laguna de Términos, Campeche, México. *An. Inst. Cienc. del Mar y Limnol., Univ. Nal. Autón. México*, **13** : 211-228.

SOLIS-WEISS., V., HERNANDEZ-ALCANTARA, P, GRANADOS-BARBA, A.,LOPEZ-GRANADOS, E., MIRANDA-VAZQUEZ, L., RODRIGUEZ- VILLANUEVA, L. V. & OCHOA-RIVERA, V., 1991. — Estudio de la macrofauna béntica : las poblaciones de anélidos poliquetos de la plataforma continental del sur del Golfo de México y su relación con el deterioro ambiental. *In* : V. SOLIS-WEISS (ed), *Dinámica oceánica y su relación con el deterioro ambiental en la porción sur del Golfo de México*. Primer Informe Técnico, Proyecto DINAMO, DGAPA/UNAM IN209789 : 135-172.

UEBELACKER, J. M. & JOHNSON, P. G., (Eds.), 1984. — *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico. Final Report to the Minerals Management Service, contract 14-12- 001-29091*. Barry A. VITTOR and Associates, Inc., Mobile, Alabama. 7 vols.

VIDAL, V. M., VIDAL, F. V., & HERNANDEZ, A. F., 1990. — *Atlas Oceanográfico del Golfo de México*. Instituto de Investigaciones Electricas, México, vol. **2**, 707 pp.

YAÑES-CORREA, E., 1971. — Procesos costeros y sedimemntos recientes de la plataforma continental al sur de la Bahía de Campeche. *Biol. Soc. Geol. Mexicana*, **32** : 75-115

Source : MNHN, Paris

# Ecological analysis of some Syllidae (Annelida, Polychaeta) from the central Tyrrhenian Sea (Ponza Island)

*A. SOMASCHINI & M. F. GRAVINA*

Dipartimento di Biologia Animale e dell'Uomo
Università "La Sapienza"
Viale dell'Università, 32 - 00185 Roma Italy

ABSTRACT

New data are given on the ecology of some syllids from soft bottom and an adjacent *Posidonia oceanica* seagrass bed in the Tyrrhenian Sea. Multivariate analysis discriminated five communities distributed along a coenocline based on granulometry of sediments, from fine to coarse sand, and from low to high shoot density within the *Posidonia* bed. Along the coenocline, replacements of some species belonging to the genera *Grubeosyllis*, *Sphaerosyllis*, *Brania*, *Exogone*, and *Syllis* were observed.

RÉSUMÉ

**Écologie de quelques Syllidae (Annelida, Polychaeta) de la partie centrale de la mer Tyrrhénienne (île de Ponza)**

On a étudié l'écologie des Syllidiens des fond meubles sableux et d'une prairie de *Posidonia oceanica* de l'Ile de Ponza (Italie-Latium). La discrimination de cinq groupements annélidiens en relation avec la structure du substrat (granulométrie des sédiments et densité des faisceaux foliaires) a permis de préciser les préférences écologiques des espèces les plus abondantes.

## INTRODUCTION

Syllids are one of the most important polychaete families in littoral communities of the Mediterranean Sea. They are the richest taxon in both abundance and species composition in rocky bottoms and seagrass beds (ABBIATI, 1987; BELLAN, 1964; COLOGNOLA *et al.*, 1984; GAMBI *et al.*, 1989; GIANGRANDE, 1985; 1988; SAN MARTIN & VIEITEZ, 1984; SAN MARTIN *et al.*, 1990), whereas in the soft bottoms they are frequently represented by many interstitial species primarily belonging to the subfamilies Exogoninae and Eusyllinae (COGNETTI, 1962;

SOMASCHINI, A. & M.F. GRAVINA, 1994. — Ecological Analysis of Some Syllidae (Annelida, Polychaeta) from the central Tyrrhenian Sea (Ponza Island) *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 567-573. Paris ISBN 2-85653-214-4.

Source : MNHN, Paris

SAN MARTIN, 1984a; 1984b; WESTHEIDE, 1974). Historical data on the ecology of this group are available in many works (e.g. BELLAN, 1964; COGNETTI, 1954; 1957; WESTHEIDE, 1974; SAN MARTIN, 1984a; GIANGRANDE, 1989-1990), but recent revisions of several genera and descriptions of many new taxa have changed the taxonomic position of many Mediterranean species (e.g. BANSE, 1971; PERKINS, 1981; SAN MARTIN, 1984a; 1984c; 1991). Furthermore, ecological information on Mediterranean syllid species is still largerly incomplete. This study presents new data based on current knowledge on the distribution and ecology of some species from soft bottoms and seagrass beds.

## MATERIALS AND METHODS

Samples were collected at Ponza Island in the central Tyrrhenian Sea (Italy-Latium) (Fig. 1). The study area, Cala Feola, is a broad bay with a bed of *Posidonia oceanica* ranging in depths from 1 m to 40 m and surrounded by soft bottom areas ranging in depths from 5 m to 40 m. Patches of dead mats (dead rhyzomes without leaf stratum) are distributed within the *Posidonia* bed. The inner part of the bay is a sheltered area of shallow water (1-2 m depth).

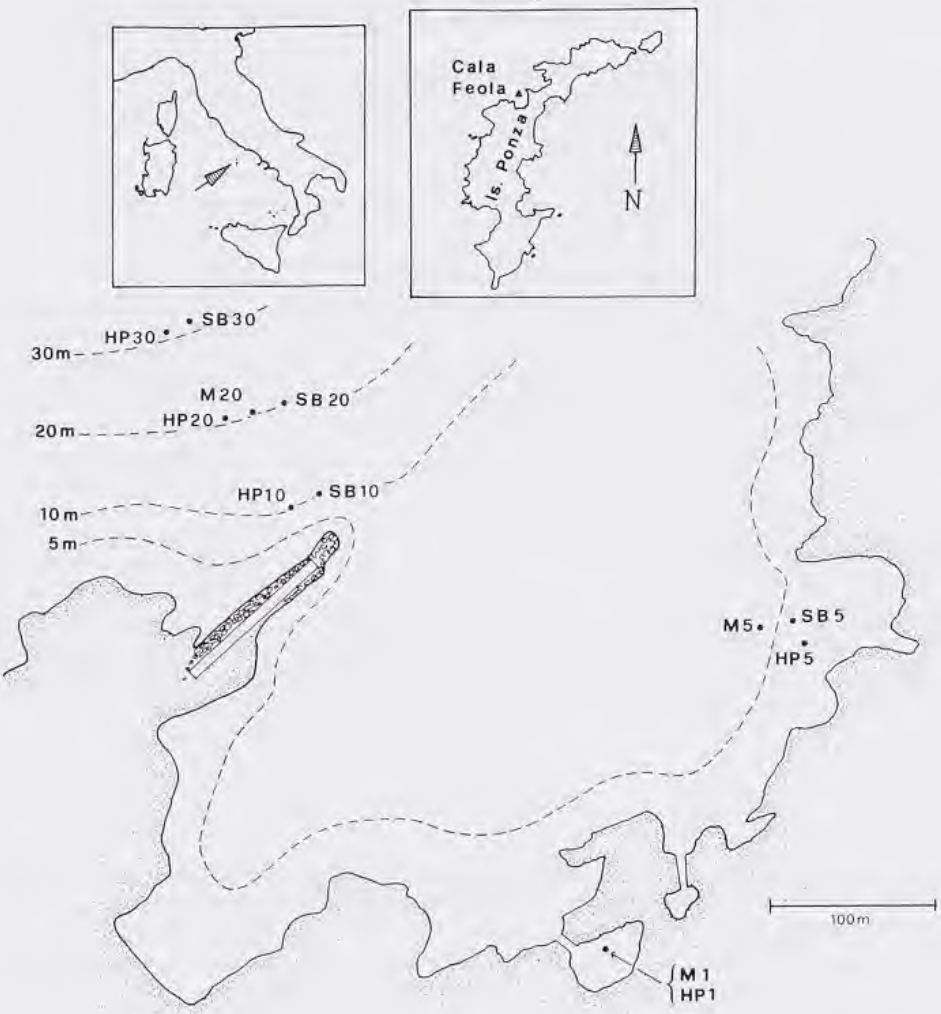



FIG. 1. — The study area. SB marks the soft-bottom sampling stations; HP those of the live *Posidonia* mat, and M the dead mat stations in the *Posidonia* bed. Numerals following letter abbreviations refer to station depths in meters.

Source : MNHN, Paris

Samples were collected in June 1988 in depths from 1 m to 30 m. Five samples were collected from a live *Posidonia* mat (HP); three samples were collected from the dead rhyzome mat (M); and four samples were collected from neighbouring soft bottom areas (SB) (Table 1). The shoot *Posidonia* density in a square meter was computed on live mat before collecting samples. The fauna of the *Posidonia* bed was collected by means of a hand net measuring 20 x 20 x 15 cm. In the live mat, fauna was collected after removing the blades of grass, whereas the dead mat fauna was collected directly. Fauna in soft bottom areas was collected with a Charcot dredge (volume: 50 l). Corers of sediment were collected in the soft bottom areas for grain size analysis (SOMASCHINI, 1992; SOMASCHINI *et al.*, in press).

TABLE 1. — Biotope features: granulometric composition of soft bottom stations (SB); shoot density values of *Posidonia* bed and exposure to water movement (HP indicates stations of live matte M indicates stations of dead mat).

| soft-bottom stations | | | SB | SB | SB | SB |
|---|---|---|---|---|---|---|
| depths (m) | | | 5 | 10 | 20 | 30 |
| grain size (mm) | | | | | | |
| > 4 | | | 00.00 | 07.08 | 00.00 | 00.00 |
| 2 | | | 00.16 | 17.29 | 00.00 | 00.00 |
| 1 | | | 00.50 | 52.70 | 00.50 | 01.32 |
| 0.5 | | | 00.55 | 22.76 | 01.36 | 03.21 |
| 0.25 | | | 51.17 | 00.12 | 30.39 | 25.59 |
| 0.12 | | | 36.00 | 00.02 | 48.12 | 48.80 |
| 0.063 | | | 10.45 | 00.01 | 19.63 | 21.08 |
| sand type | | | fine | coarse | fine | fine |
| *Posidonia* stations | HP | M | HP M | HP | HP M | HP |
| depth (m) | 1 | 1 | 5 5 | 10 | 20 20 | 30 |
| Shoot density (square meter) | 710 | 0 | 780 0 | 750 | 518 0 | 304 |
| Exposure to water movement | NO | NO | YESYES | YES | NO NO | NO |

Frequency data of the total polychaete fauna at each station were computed and logarithmically transformated. Principal Component Analysis (PCA) was employed on the correlation matrix to order the sampling stations (SOMASCHINI *et al.*, in press). In the obtained ordination model, Euclidean distances were computed between the sampling station points, to order them along the principal coenocline. This coenocline was used in order to study the distribution patterns of the most abundant syllids. Only syllids with a frequency higher than 1% of the total polychaete fauna were analyzed. The distribution patterns along the coenocline of the selected species were studied computing the weighted mean of three successive sets of data (CURTIS & McINTOSH, 1951; GAUCH, 1982). Additional details on the mathematical methods used in this study can be found in SOMASCHINI (1992).

## RESULTS AND CONCLUSIONS

A total of 15,232 individuals belonging to 218 species of polychaetes was found (SOMASCHINI, 1992). Syllidae were the richest family in both abundance and species richness (7,381 individuals and 76 species). Three new species of Syllids were described and a new report for the Mediterranean Sea was carried out (SOMASCHINI, 1992). Exogoninae and Syllinae were very abundant and diverse in the *Posidonia* bed, whereas from the soft bottom only Eusyllinae and Exogoninae were collected.

Multivariate analysis on the total fauna discriminated five communities related to sediment type, *Posidonia* shoot density, and the exposure to water movement (SOMASCHINI *et al.*, in press). Communities of fine sand (5 + 20 + 30 m) and of coarse sand (10 m) were identified in the soft bottom areas. A community was found in the deeper *Posidonia* samples with a low shoot density (20 + 30 m), whereas two communities were found in the

Source : MNHN, Paris

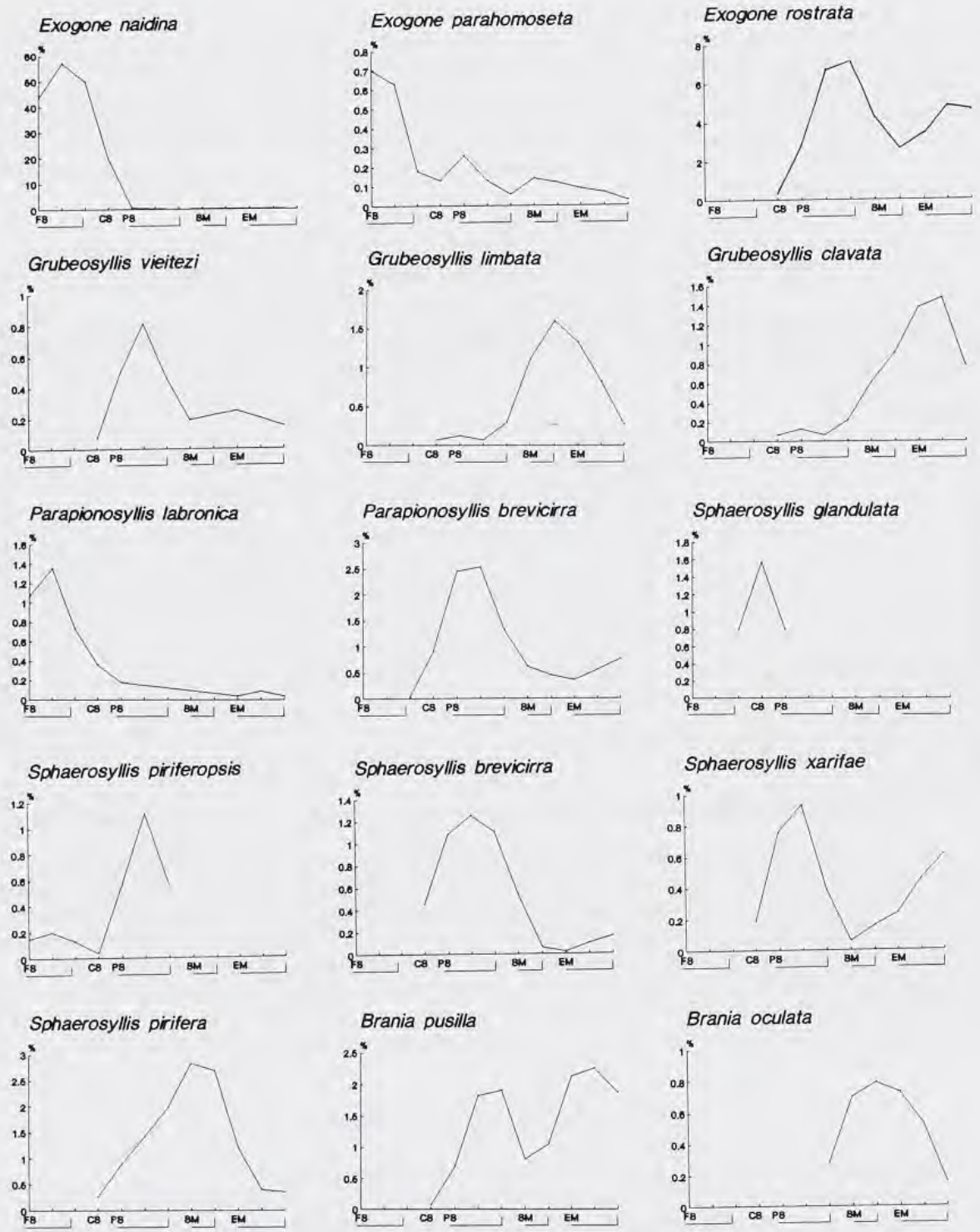



FIG. 2. — Percent distribution of the most abundant syllid species (frequency on total polychaete fauna > 1%) along the ecological gradient observed. On the horizontal axis: FS = fine sand (SB20; SB30; SB5); CS = coarse sand (SB10); PS = deep *Posidonia* bed (HP20; HP30; M20); SM = sheltered shallow *Posidonia* mat (1PS; 1M); EM = exposed *Posidonia* mat (5PS; 5M; 10PS).

Source : MNHN, Paris

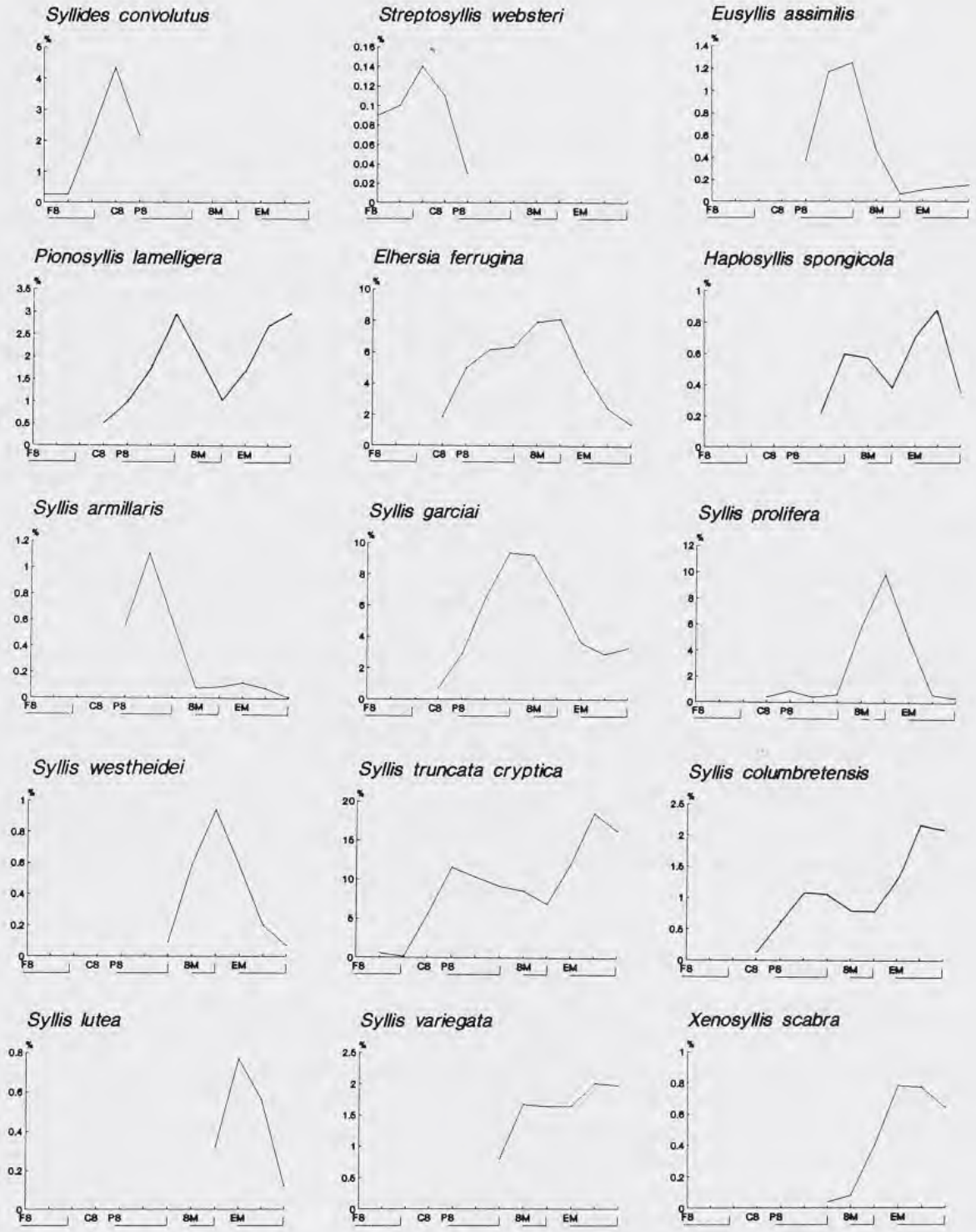



FIG. 2 (continued). — Percent distribution of the most abundant syllid species (frequency on total polychaete fauna > 1%) along the ecological gradient observed. On the horizontal axis: FS = fine sand (SB20; SB30; SB5); CS = coarse sand (SB10); PS = deep *Posidonia* bed (HP20; HP30; M20); SM = sheltered shallow *Posidonia* mat (1PS; 1M); EM = exposed *Posidonia* mat (5PS; 5M; 10PS).

shallow *Posidonia* bed with high shoot density (1 + 5 + 10 m depth), respectively on sheltered (1 m) and exposed (5 + 10 m depth) habitats.

Source : MNHN, Paris

Euclidean distances ordered the sampling stations along a coenocline from fine to coarse sand, and within the *Posidonia* bed from low to higher shoot densities and water movement exposure (SB20; SB30; SB5; SB10; HP20; HP30; M20; 1PS; 1M; 5PS; 5M; 10PS). Distributions of the most abundant syllids (frequency > 1%) along the ecological gradients are shown in figure 2. Detailed results of the study can be found in SOMASCHINI (1992).

The fine sand was inhabited by a few dominant species, such as *Exogone naidina* Örsted and *Parapionosyllis labronica* Cognetti. Apparently, the presence of many interstices in the coarse sand made the sediment more similar to the mat samples and suitable for many syllids (e.g. *Sphaerosyllis glandulata* Perkins, *Sphaerosyllis taylori* Perkins, *Syllides convolutus* Webster & Benedict, and *Streptosyllis websteri* Southern as dominant species).

In the shallower stations (1 + 5 m depth) of the *Posidonia* bed, the polychaete community changed according to the exposure to water movement (SOMASCHINI, 1992). The sheltered stations (1 m depth) of the *Posidonia* bed were inhabited by many species known to be associated with the sediment deposition, such as *Syllis garciai* Campoy, *Syllis prolifera* Krohn, *Sphaerosyllis pirifera* Claparède, and *Elhersia ferrugina* Langerhans. The same species were also present in the deepest stations (20 + 30 m) among the more sparse *Posidonia* rhizomes. Other syllid species, such as *Pionosyllis lamelligera* Saint-Joseph, *Sphaerosyllis xarifae* Hartmann-Schröder, *Exogone rostrata* Naville and *Brania pusilla* Dujardin occurred more abundantly at the shallower stations of the *Posidonia* bed which, however, were more exposed to water movement (5 + 10 m depth). *Pionosyllis lamelligera* and *Brania pusilla* are commonly reported for shallow rocky bottoms, whereas *E. rostrata* is reported for sciaphilic algal communities (ABBIATI *et al.*, 1987; NUNEZ *et al.*, 1992).

In the literature many syllid species are reported to have broad distributions on rocky as well as in soft, littoral substrata (BELLAN, 1964; BELLAN-SANTINI, 1969). The current data give more detailed information about the autoecology of some of these species in that a replacement of some congeneric species along the coenocline was observed (Fig. 2). Among the Exogoninae, *Grubeosyllis vieitezi* San Martin, *Grubeosyllis limbata* Claparède and *Grubeosyllis clavata* Claparède substituted for each other in relation to the different conditions within the *Posidonia* bed. *G. vieitezi* was more abundant in the deep *Posidonia* samples, whereas *G. limbata* and *G. clavata* were more abundant in shallow waters with high shoot density, in sheltered and exposed conditions respectively. In the genus *Brania*, *B. pusilla* occurred more abundantly in the deepest stations of the *Posidonia* bed as well as at the more exposed ones, whereas *B. oculata* Hartmann-Schröder was quite abundant in the sheltered *Posidonia* habitat. In the genus *Syllis*, *S. prolifera* and *Syllis westheidei* San Martin were more abundant in the shallowest sheltered area; *S. garciai* occurred more abundantly in the deeper *Posidonia* bed with low shoot density, whereas *Syllis variegata* Grube and *Syllis columbretensis* Campoy were more abundant in the more exposed *Posidonia* environment. In the shallowest sheltered area, *Sphaerosyllis pirifera* substituted for *Sphaerosyllis xarifae*, *Sphaerosyllis brevicirra* Hartmann-Schröder and *Sphaerosyllis piriferopsis* Perkins which, however, were common at the other stations of the *Posidonia* bed. Only *Sphaerosyllis glandulata* was a characteristic species of the coarse sand stations. Finally, in fine sand, *Exogone parahomoseta* Hartmann-Schröder and *Exogone naidina* replaced *Exogone rostrata*, typically recorded in *Posidonia* beds.

## REFERENCES

ABBIATI, M., 1987. — Policheti di fondo roccioso del promontorio di Romito (Livorno). *Atti Soc. Tosc. Sci. Nat. Mem.* Serie B, **94** : 215-233.

ABBIATI, M., BIANCHI, C. N. & CASTELLI, A. 1987. — Polychaete Vertical Zonation along a Littoral Cliff in the Western Mediterranean. *P.S.Z.N.I. Marine Ecology*, **8** : 33-48.

BANSE, K., 1971. — A new species and addition to the description of six other species of *Syllides* Örsted (Syllidae: Polychaeta). *J. Fish. Res. Board. Canada*, **28** : 1469-1481.

BELLAN, G., 1964. — Contribution à l'étude systématique bionomique et écologique des Annélides Polychètes de la Méditerranée. *Rec. Trav. St. mar. Endoume*, **49** (33) : 1-372.

BELLAN SANTINI, D., 1969. — Contribution à l'étude des peuplements infralittoraux sur substrat rocheux (étude qualitative et quantitative de la frange supérieure). *Rec. Trav. St. mar. Endoume*, **47** (63) : 1-294.

COGNETTI, G., 1954. — Ricerche sui Sillidi del Golfo di Napoli. *Publ. Staz. Zool. Napoli*, **26** : 1-11.

COGNETTI, G., 1957. — I Sillidi del Golfo di Napoli. *Publ. Staz. Zool. Napoli*, **30** : 1-100.

COGNETTI, G., 1962. — I Policheti dei fondi a sabbia grossolana del litorale livornese. *Boll. Zool.*, **29** : 1-7.

Source : MNHN, Paris

COLOGNOLA, R., CHESSA, C. A., FRESI, E., RUSSO, G.F., PETRINI, L., 1984. — Zoobenthos della rada di Palau (Sardegna) : I Syllidae (Polychaeta). *Nova Thalassia*, **6** (suppl.) : 569-574.

CURTIS, J. T.& McINTOSH, R. P., 1951. — An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, **32** : 476-496.

GAMBI, M.C., GIANGRANDE, A., CHESSA, L. A., MANCONI, R., SCARDI, M., 1989. — Distribution and ecology of Polychaetes in the foliar stratum of a *P. oceanica* bed in the bay of Porto Conte. *In* : C.F. BOUDOURESQUE, A. MEINESZ, E. FRESI & V. GRAVEZ (éds.), *International Workshop Posidonia oceanica Beds*, GIS Posidonie publ., Fr., **2** : 175-188.

GAUCH, H.G., Jr. 1982. — *Multivariate analysis in community ecology*. Cambridge studies in ecology, Cambridge University Press : 298 pp.

GIANGRANDE, A., 1985. — Policheti dei rizomi di *P. oceanica* L. Delile di una prateria dell'isola di Ischia (Napoli). *Atti Soc. Tosc. Sci. Nat. Mem.* ser.B, **92** : 195-206.

GIANGRANDE, A., 1988. — Polychaete zonation and its relation to algal distribution down a vertical cliff in the western Mediteranean (Italy) : a structural analysis. *J. exp. mar. Biol. Ecol.*, **120** : 263-276.

GIANGRANDE, A., 1989/90. — Distribution and reproduction of syllids (Annelida, Polychaeta) along a vertical cliff (West Mediterranean). *Oebalia*, **16**, N.S.: 69-85.

NUNEZ, J., SAN MARTIN, G. & DEL CARMEN BRITO M., 1992. — Exogoninae (Polychaeta: Syllidae) from Canary Islands. *Sci. Mar.*, **56** : 43-52.

PERKINS, T.H., 1981. — Syllidae (Polychaeta), principally from Florida, with description of a new genus and twenty-one new species. *Proc. Biol. Soc. Wash.*, **93** : 1080-1172.

SAN MARTIN, G., 1984a. — *Estudio biogeografico, faunistico y sistematico de los Poliquetos de la familia Silidos (Syllidae : Polychaeta) en Baleares*. Doctoral Thesys. Ediciones de la Universidad Complutense de Madrid, n° 187 : 1-529.

SAN MARTIN, G., 1984b. — Biogeography of the Syllidae (Polychaeta) from the Spanish Mediterranean Coasts. *In*: P. A. HUTCHINGS (ed.), *Proceedings of the First International Polychaete Conference*. Linnean Society of New South Wales : 303-322.

SAN MARTIN, G., 1984c. — Descripcion de una nueva especie y revision del genero *Sphaerosyllis*. *Cah. Biol. Mar.*, 25 : 375-392.

SAN MARTIN, G., 1991. — *Grubeosyllis* and *Exogone* (Exogoninae, Syllidae, Polychaeta) from Cuba, the Gulf of Mexico, Florida and Puerto Rico, with a revision of *Exogone*. *Bull. Mar. Sci.*, **49** : 715-740.

SAN MARTIN G. & VIEITEZ J.M., 1984. — Anelidos poliquetos de los rizomas de *Posidonia oceanica* en las costas del Cabo de Palos (Murcia, Espana). *In* : C.F. BOUDOURESQUE, A. JEUDY DE GRISSAC & J. OLIVIER (éds.), *International workshop on Posidonia oceanica beds*, GIS Posidonie publ.: 149-157.

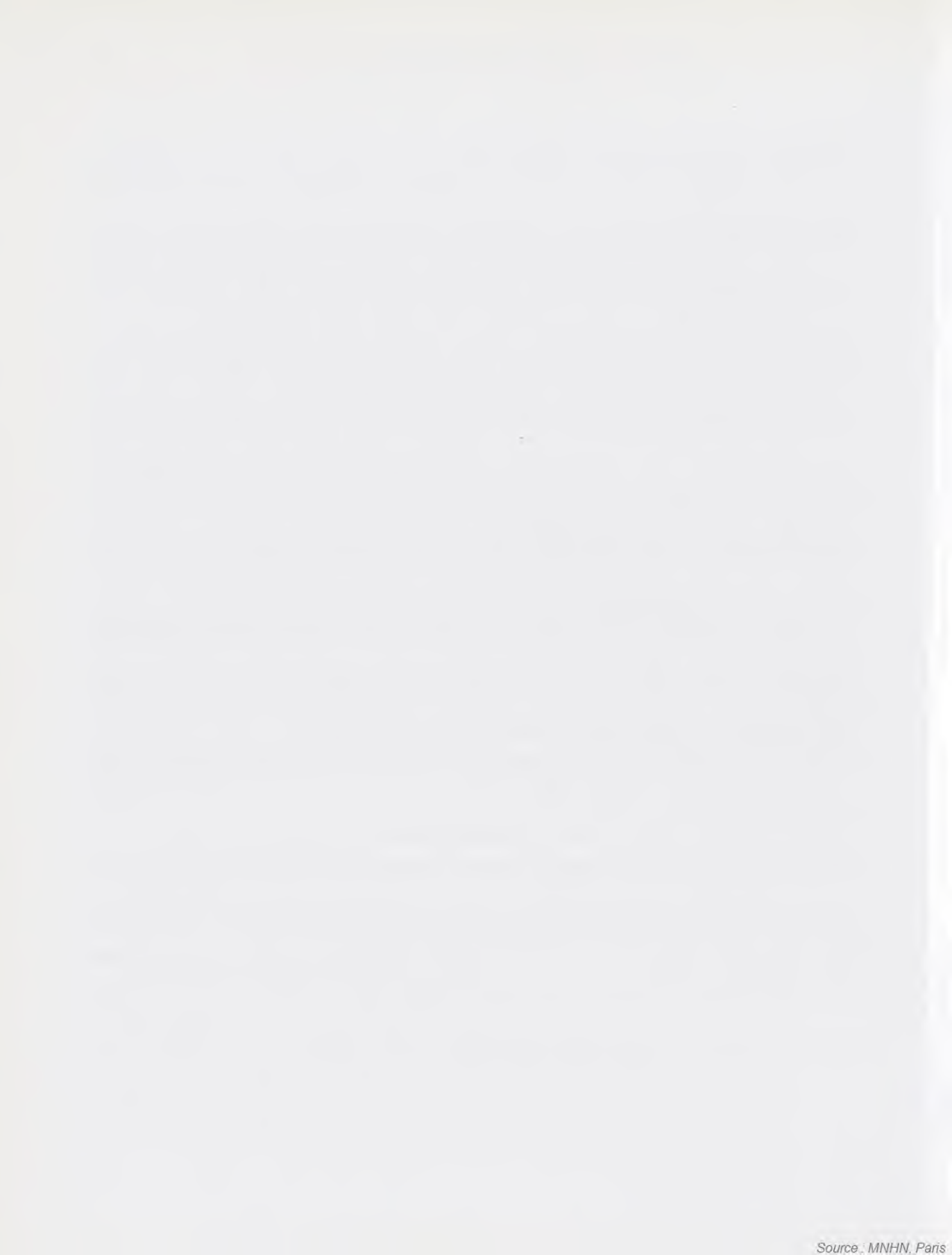
SAN MARTIN G., ESTAPE S., GARCIA-OCEIO A., GOMEZ C. & JIMENEZ P., 1990. — Estudio de la taxocenosis de Anelidos Poliquetos de rizomas de *Posidonia oceanica* en la costas de Almeria. *Bol. Inst. Esp. Oceanogr.*, **6** : 41-58.

SOMASCHINI, A., 1992. — *Analisi strutturale e funzionale del popolamento ad Anellidi Policheti di una prateria di Posidonia oceanica (strato dei rizomi)*. Unpublished Doctoral Thesis, University "La Sapienza" of Rome , 90 pp.

SOMASCHINI, A., GRAVINA, M. F., ARDIZZONE, G. D., in press. — Polychaete depth distribution in a *P. oceanica* bed (rhizome and matt strata) and neighbouring soft and hard bottoms. *P.S.Z.N.I. Marine Ecology*.

WESTHEIDE, W., 1974. — Interstitielle fauna von Galapagos. XI Pisionidae, Hesionidae, Pilargidae, Syllidae. *Mikrofauna Meeresbodens*, **44** : 195-338.

Source : MNHN, Paris



Source : MNHN, Paris

# Cyclical changes in the fauna associated with tube aggregates of *Ficopomatus enigmaticus* (Fauvel)

*Nigel S. THOMAS* & Clifford H. THORP***

* Southern Science Ltd., Hampshire Laboratory
Otterbourne, Hants, SO21 2SW, U.K.
** University of Portsmouth, School of Biological Sciences, Marine Laboratory
Ferry Rd., Hayling Island, Hants, PO11 0DG, U.K.

ABSTRACT

Studies were undertaken on the fauna associated with the tube aggregations of *Ficopomatus enigmaticus* in a brackish water lagoon, in southern England, from 1982–1992. During this time a population crash and partial recovery was observed. Aggregates, consisting of living animals, were occupied in abundance by the amphipods *Leptocheirus pilosus*, *Corophium insidiosum* and *Melita palmata*, with numbers declining in dead colonies. Initially moribund aggregates were invaded in large numbers by the isopod *Lekanesphaera hookeri*. At the same time the polychaete *Hediste (Nereis) diversicolor* showed an increase in numbers. *Leptocheirus pilosus* returned in abundance by 1989. The fluctuations in associated species were related to the ability of *F. enigmaticus* to prevent deposition and accumulation of sediment and organic material. Parallel sampling of the adjoining muddy sediments revealed catastrophic disappearance and re-appearance of species, similar to that shown by *F. enigmaticus*. These included the rare lagoonal polychaete, *Alkmaria romijni*. Both living and dead aggregates of *F. enigmaticus* provide an extensive benthic sub-habitat. The living aggregates may also regulate invertebrate food resources. The ecology of the benthos was controlled by the interaction of this factor with variables such as saline intrusion.

RÉSUMÉ

**Changements cycliques de la faune associée aux agrégats de tubes de *Ficopomatus enigmaticus* (Fauvel)**

Des études ont été entreprises sur la faune associée aux agrégats de tubes de *Ficopomatus enigmaticus* dans une lagune d'eau saumâtre au sud de l'Angleterre de 1982 à 1992. Au cours de cette période, on a observé la disparition puis la reconstitution partielle de la population de *F. enigmaticus*. Les agrégats constitués par des animaux vivants étaient colonisés en abondance par les amphipodes *Leptocheirus pilosus*, *Corophium insidiosum* et *Melita palmata*, dont le nombre décroissait dans les agrégats morts. Les agrégats de moribonds ont été initialement, envahis, en grand nombre, par l'isopode *Lekanesphaera hookeri*. Simultanément, les polychètes *Hediste (Nereis) diversicolor* ont montré une très forte augmentation numérique. *Leptocheirus pilosus* à retrouvé une grande abondance en 1989. Les fluctuations des espèces associées sont liées à la capacité de *F. enigmaticus* d'empêcher le dépôt et l'accumulation de sédiments et de matière organique. Des échantillons, prélevés simultanément sur les sédiments vaseux voisins, ont révélé une disparition catastrophique puis une réapparition d'une faune similaire à celle déja rencontrée dans les agrégats de *F. enigmaticus*. L'espèce lagunaire, *Alkmaria romijni*, espèce rare, a été récoltée dans ces échantillons. Les deux types d'agrégats vivants et morts de *F. enigmaticus* fournissent un large sous-habitat

THOMAS, N.S. & C.H. THORP, 1994. — Cyclical changes in the fauna associated with tubes aggregates of *Ficopomatus enigmaticus* (Fauvel) *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 575-584. Paris ISBN 2-564783-165-2.

Source : MNHN, Paris

benthique. Les agrégats vivants peuvent réguler les ressources en nourriture des invertébrés. L'écologie du benthos était contrôlée par l'interaction de ce facteur avec des variables telles que les intrusions salines.

## INTRODUCTION

FAUVEL (1933), in describing the distribution of the serpulid *(Mercierella) Ficopomatus enigmaticus*, frequently mentioned the varied fauna associated with the aggregated tubes. Observations by FISCHER–PIETTE (1925, 1928), BERTRAND (1938), RULLIER (1943), EUZET & PUJOL (1963) and VUILLEMIN (1965) showed that this associated fauna was similar in species composition. The sessile species were generally limited to a few species of bryozoa, *Balanus* and ascidians. In contrast the mobile fauna were quite diverse, consisting mainly of amphipods, isopods and polychaetes. There was a high degree of uniformity in the family groups observed, although the species frequently vary. Principal amongst these were species of *Corophium*, *Gammarus* and *Lekanesphaera (Sphaeroma)*. The amphipod *Leptocheirus pilosus* Zaddach, 1844 appeared to be almost universally found. Spatial and temporal variation in species composition has been observed by RULLIER (1943) and EUZET & PUJOL (1963), and related to fluctuations in local conditions and the health of the aggregates.

The populations of *F.enigmaticus* in the brackish water of the Emsworth, Slipper and Peter, millpond complex (Fig. 1) have been investigated since 1982 by THORP (1987, 1994). These studies have revealed considerable population variations, with a "crash" occurring in 1986, consisting of the apparent death of the adult population and a massive reduction in larval settlement. This event was followed in 1989–91 by a recovery in larval settlement, with some aggregates demonstrating regeneration and others appearing as new aggregates on the mud surface. The population decline was attributed to the age of the adult population, lack of overwintering reserves and a failure of recruitment (THORP, 1992). The last two are regulated by phytoplankton levels during summer, which in turn are controlled by sunlight, temperature and salinity. Recruitment success was also thought to depend on availability of suitable substrata for settlement.

The millpond complex in Emsworth (Fig. 1) has a combined area of 2.7 hectares and, apart from a deeper water entrance and channel, a maximum depth of less than 1.5 m (THORP, 1987). Seawater enters on high spring tides from Chichester Harbour, through tide gates at the southern end. Fresh water enters from the River Ems in the north. Winter and spring bottom salinities vary from 0 to 30 and summer to autumn salinities are normally from 10 to 34. The substratum is composed of silty muds (median diameter 0.022 mm to 0.047 mm) and high levels of organic material (9 % to 16 %) (unpublished data), although stones and other hard substrata, such as broken bottles, are scattered over the surface. These hard objects are the surfaces upon which the aggregations of *F. enigmaticus* occur.

Concurrent with the study by THORP (1994) on fluctuations in the population of *F. enigmaticus*, the opportunity was taken to determine how the associated fauna varies with the health of the aggregates. The present paper describes and attempts to explain some of the changes observed, and relates these to the benthic faunal communities of the millpond complex.

## MATERIALS AND METHODS

Samples of sediment and aggregates of *F. enigmaticus* were collected in the autumns of 1982, 1987, 1989 and 1991. On each occasion at least five small aggregates of *F. enigmaticus* were collected, with volumes between 0.5 and 1.5 litres. At the same time two cores (9 cm diameter x 15 cm deep) of mud were collected from each of five sites (Fig. 1). Additional cores were collected, in the latter three years, for the analysis of sediment particle size and organic material content. All the samples were taken to the laboratory where the aggregates were frozen and the sediment samples sieved through a 0.5 mm mesh.

Each frozen aggregate was measured by placing it into a plastic bag and then plunging it into a Eureka can to determine the volume. The plastic bag was then removed and the volume measured again. A final volume was taken once all the sediment had been washed from the aggregate. It was possible then to calculate the interstitial space and the percentage of that space occupied by sediment. The sediment removed from the aggregates was also washed through a 0.5 mm sieve and all animals sorted, preserved and identified to species where possible.

Particle size analysis was undertaken using an initial wet sieving technique followed by dry sieving of the $> 0.063$ mm fraction and wet suspension of the $< 0.063$ mm fraction; organic content was estimated by loss on ignition (HOLME & MCINTYRE, 1971).

Source : MNHN, Paris

## RESULTS

The full species list for both aggregates and adjacent sediment is given in Table 1, showing the composition and abundance of the species, in both the aggregates and the sediment, over the four sampling periods. The changes in the species numbers are demonstrated in Figure 2. There is an apparent inverse relationship between the number of species in the aggregates and in the sediments. The number of species was greatest in theaggregates in the period 1987 to 1989. This period corresponds to the lowest species numbers in the sediment. The reverse was true in 1982 and 1991, although species numbers in the 1991 aggregates were relatively high.

The state of health of the aggregates can be seen to be related to the number of species and abundance of individuals (Fig. 3). Although lower species numbers occurred in the live aggregates, they supported a greater number of individuals. The physical condition of the aggregates can be related, to some extent, to the quantity of sediment they contain. Figure 3 demonstrates that greater quantities of sediment occupied the dead and regenerating aggregates with levels as high as 40% in the latter.

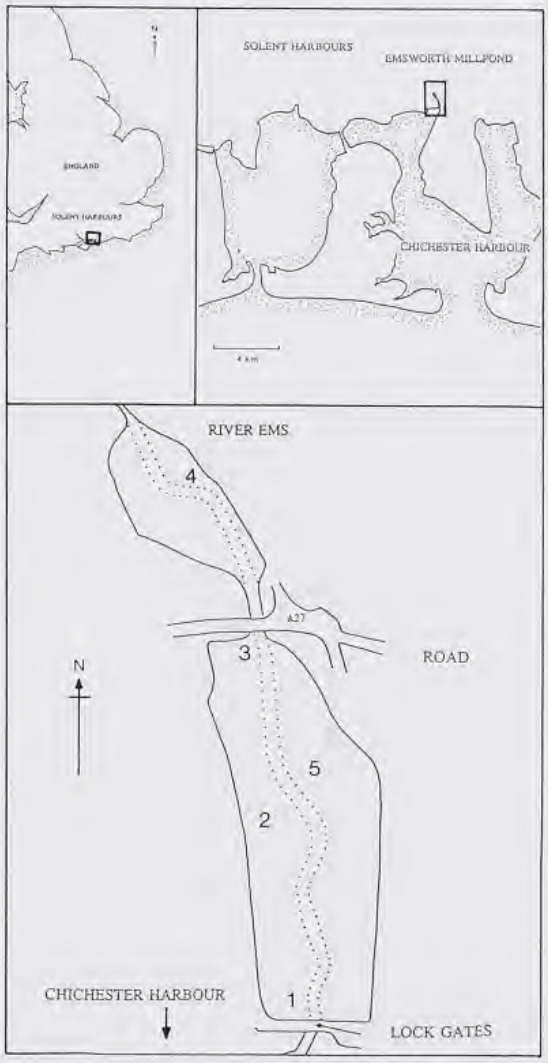



FIG. 1. — Sampling sites in the Emsworth millpond complex, with its location indicated in the Solent Harbours system, on the south coast of England.

Source : MNHN, Paris

TABLE 1. — List of fauna associated with live, dead and regenerating *Ficopomatus* aggregates (Agg) and in the mud of the Emsworth millpond complex. *: low abundance, **: medium abundance, ***: high abundance.

| Species | 1982 | Live | 1987 | Dead | 1989 | Dead | 1991 | Regen. |
|---|---|---|---|---|---|---|---|---|
| | Agg | Mud | Agg | Mud | Agg | Mud | Agg | Mud |
| Anthozoa | | | | | | | | |
| Actiniria | | | | | | | | |
| *Nematostella vectensis* | - | *** | - | - | - | - | - | - |
| Annelida | | | | | | | | |
| Oligochaeta | | | | | | | | |
| *Tubificoides benedeni* | - | ** | * | - | - | - | - | - |
| Oligochaete indet. | - | - | - | - | - | - | - | * |
| Polychaeta | | | | | | | | |
| *Eteone longa* | - | *** | - | - | - | - | - | * |
| *Nereis diversicolor* | * | ** | *** | *** | ** | *** | ** | *** |
| *Alkmaria romijni* | - | ** | * | ** | - | - | - | *** |
| *Streblospio shrubsoli* | - | * | * | - | ** | *** | - | *** |
| *Polydora ciliata* | - | * | - | - | ** | ** | * | * |
| Spionid indet. | - | - | * | * | ** | ** | - | * |
| *Capitella* sp. | - | * | * | - | - | - | - | - |
| *Tharyx marioni* | - | * | - | - | - | - | - | - |
| *Manayunkia aestuarina* | - | * | - | - | - | - | - | - |
| Crustacea | | | | | | | | |
| Cirripedia | | | | | | | | |
| *Balanus improvisus* | - | - | - | - | * | - | - | - |
| Amphipoda | | | | | | | | |
| *Leptocheirus pilosus* | *** | * | * | - | *** | - | *** | ** |
| *Melita palmata* | *** | ** | * | - | *** | - | * | * |
| *Gammarus zaddachi* | - | - | ** | - | - | - | - | - |
| *Gammarus salinus* | - | - | ** | - | - | - | - | - |
| *Gammarus locusta* | - | - | - | - | * | - | - | - |
| *Gammarus duebeni* | - | - | - | - | - | - | * | - |
| *Corophium insidiosum* | *** | - | - | - | - | - | - | - |
| *Corophium volutator* | - | ** | - | - | * | - | - | * |
| *Jassa falcata* | - | * | - | - | - | - | - | * |
| Isopoda | | | | | | | | |
| *Lekanesphaera hookeri* | - | - | *** | ** | * | - | *** | * |
| *Cyathura carinata* | - | ** | * | ** | ** | *** | *** | *** |
| Tanaidacea | | | | | | | | |
| *Heterotanais oerstedi* | - | - | - | - | *** | - | * | - |
| Decapoda | | | | | | | | |
| *Carcinus maenas* | * | - | * | - | * | - | * | - |
| Mollusca | | | | | | | | |
| Gastropoda | | | | | | | | |
| *Hydrobia ulvae* | - | - | - | - | - | - | * | * |
| Pelecypoda | | | | | | | | |
| *Cerastoderma edule* | - | * | - | - | * | - | ** | ** |
| *Ostrea edulis* | - | - | - | - | - | - | * | - |
| *Mya arenaria* | - | - | - | - | - | * | - | * |
| Ascidiacea | | | | | | | | |
| *Ascidiella aspersa* | - | - | - | - | * | - | - | - |
| *Ciona intestinalis* | - | - | - | - | * | - | - | - |
| Total N°. Species | 5 | 16 | 13 | 5 | 16 | 6 | 12 | 16 |

The principal species found in the aggregates show clear differences in abundance between aggregate types (Fig. 4). The live aggregates were co–dominated by the amphipods *Leptocheirus pilosus*, *Corophium insidiosum*

Source : MNHN, Paris

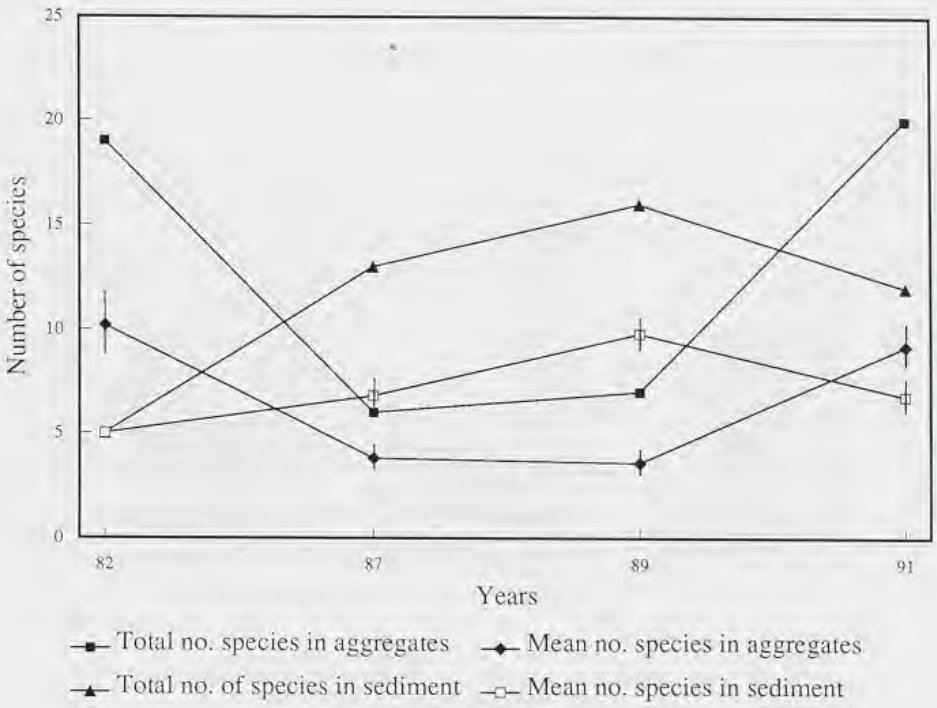



FIG. 2. — Mean and total number of species in the aggregates and in the sediment, 1982–91. (mean number of species ± s.e.).

Crawford, 1937 and *Melita palmata* (Montagu, 1804). The former species dominated in all aggregate types, whereas *C. insidiosum* occurred only in live aggregates. Several other species, but most noticably *Lekanesphaera hookeri* (Leach, 1814), *Cyathura carinata* (Kröyer, 1847) and *Hediste diversicolor* (O.F. Müller, 1776) were found in the greatest numbers in dead or regenerating aggregates, although all were found in the live aggregates on at least one occasion. *L. hookeri* and *H. diversicolor* in particular dominated the dead aggregates during 1987.

By further examining the changes in abundance that have occurred over the 10 year period and comparing these with Figure 4, it is possible to determine whether the state of health of the aggregates is the most important influencing factor. Figure 5 confirms that *L. pilosus* and probably *M. palmata* have responded to factors in addition to the collapse in the health of the aggregates, with low values occurring in 1987 followed by high values in 1989, both periods when dead aggregates were prevalent. *C. insidiosum* in contrast disappeared by 1987 and failed to re–appear, indicating that it may have been specific to live aggregates.

Of the secondary dominants, the three species *L. hookeri, C. carinata* and *H. diversicolor* all showed increases in abundance after the disappearance of the live aggregates (Fig. 6). This has been most pronounced for *L. hookeri* which was the dominant aggregate species in 1987. The changes in *C. carinata* and *H. diversicolor* have been less dramatic but were greatest in the period 1982 to 1987. Both of these species have stayed at relatively uniform levels in the adjacent mud (Fig. 7) suggesting that the death of the aggregates could be the most important factor influencing the changes observed.

The stability of *H. diversicolor* and *C. carinata* in the mud contrasts with several other species that were abundant in the sediments (Fig. 8). The polychaete species *Streblospio shrubsoli* (Buchanan, 1890) and *Alkmaria romijni* Horst, 1919 have undergone considerable variations. An equally large change has also been shown by the anthozoan *Nematostella vectensis* Stephenson, 1935 which disappeared by 1987 and was not found subsequently.

Data on the sediment particle size and organic material levels have not been complete over the 10 year period but there has been no evidence of long term changes in either. Percentage sediment less than 0.063 mm in diameter has been recorded as between 60 to 80 % and organic material at an almost uniform 13 %.

Source : MNHN, Paris

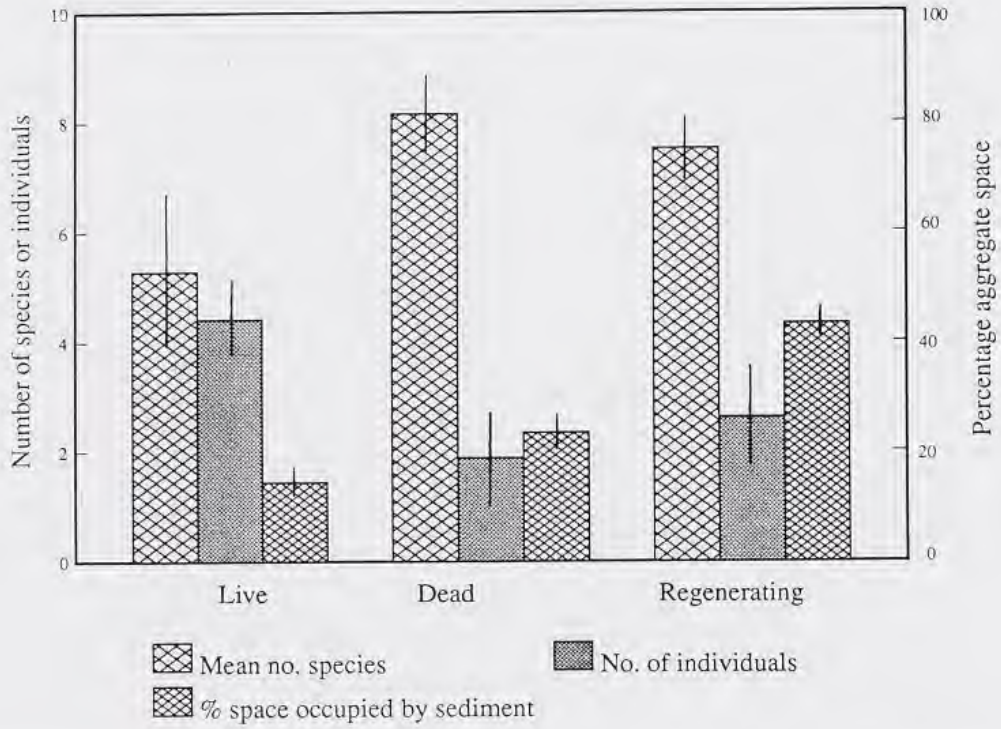



FIG. 3. — Species number, abundance and percentage interstitial sediment in live, dead and regenerating aggregates. (species numbers are means ± s.e.,abundances are mean numbers per $cm^3$ ± s.e. and percentage is mean ± s.e.).

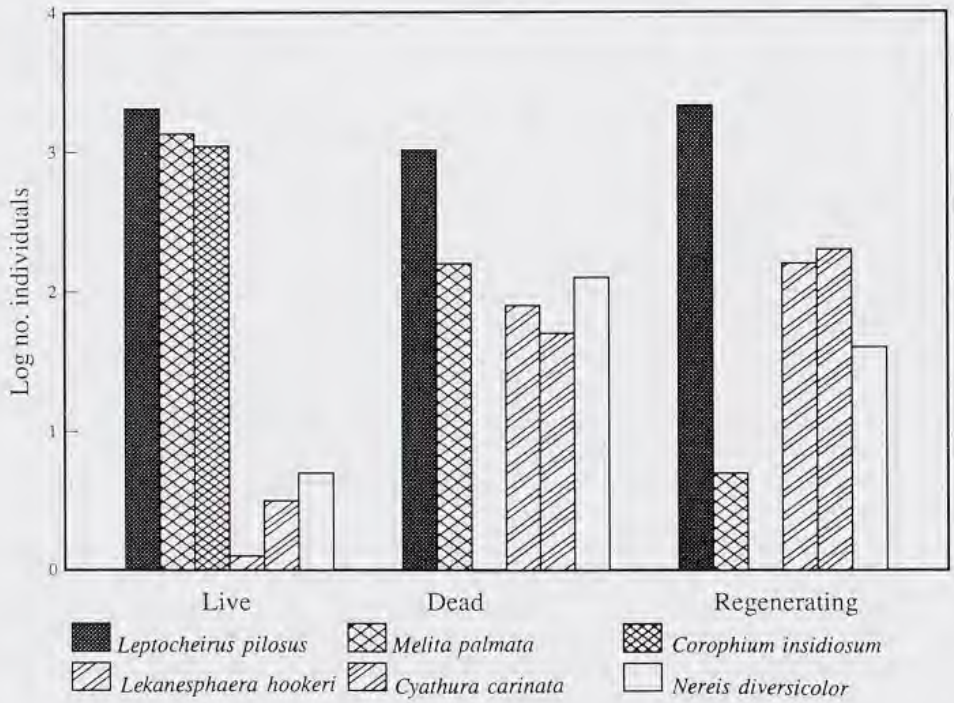



FIG. 4. — Abundance of dominant species in different aggregate types. (mean number of individuals per litre).

Source : MNHN, Paris

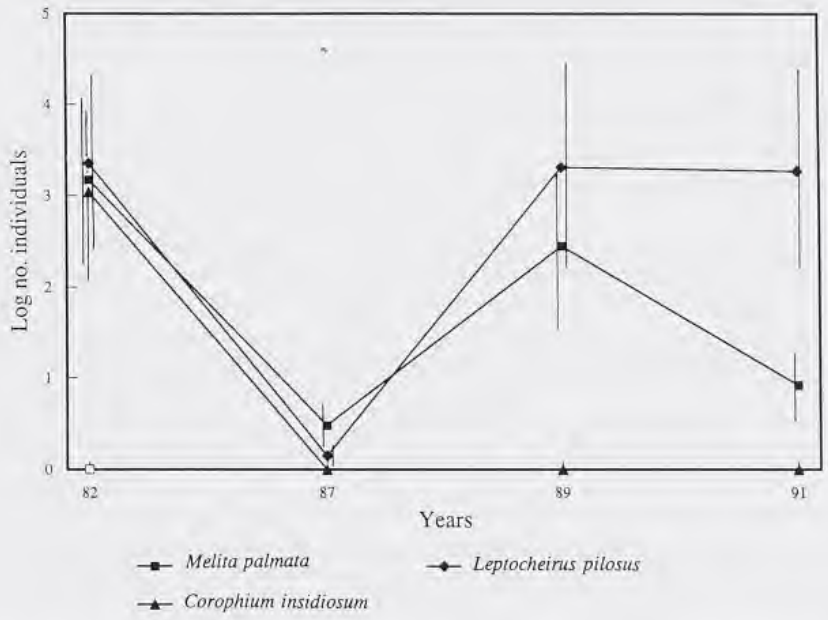



FIG. 5. — Changes in the abundance of dominants in aggregates. ($log_{10}$, mean number of individuals per litre ± s.e.).

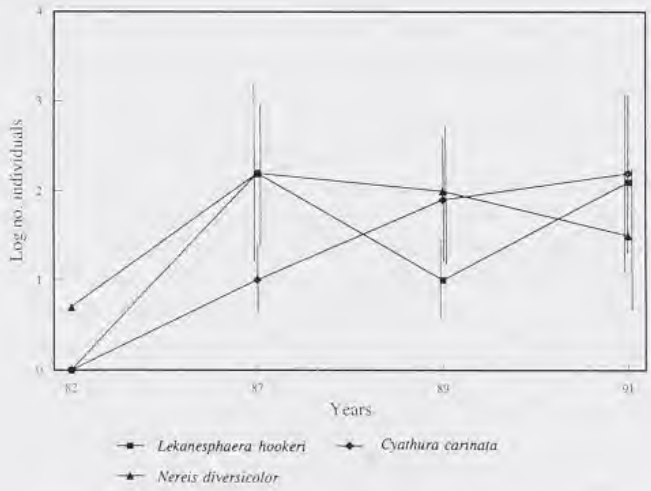



FIG. 6. — Changes in abundance of secondary dominants in aggregates. ($log_{10}$, mean number of individuals per litre ± s.e.).

## DISCUSSION

Two of the most commonly occurring species in the live aggregates of *F. enigmaticus*; *L. pilosus* and *C. insidiosum*, are tubicolous amphipods (LINCOLN, 1979) which exploit particulate material suspended in moving water, such as that found in the millponds complex. They are unable to tolerate the high silt and clay levels in the sediments, which are more suited to the burrowing polychaetes and crustaceans. Both species were found by GOODHART (1939), living in a brackish water sluice pond, similar to the millpond. There *L. pilosus* constructed its tubes on the thallus of *Chondrus crispus* thus remaining in moving water above the soft sediment floor. *C. insidiosum* has also been found by SHEADER (1978) in high turbidity waters associated with mats of *Rhodochorton*

Source : MNHN, Paris

sp. *M. palmata* differs in that it is normally found amongst stones and gravel in silty environments (LINCOLN, 1979) and is probably occupying the silt filled areas at the base of the aggregations.

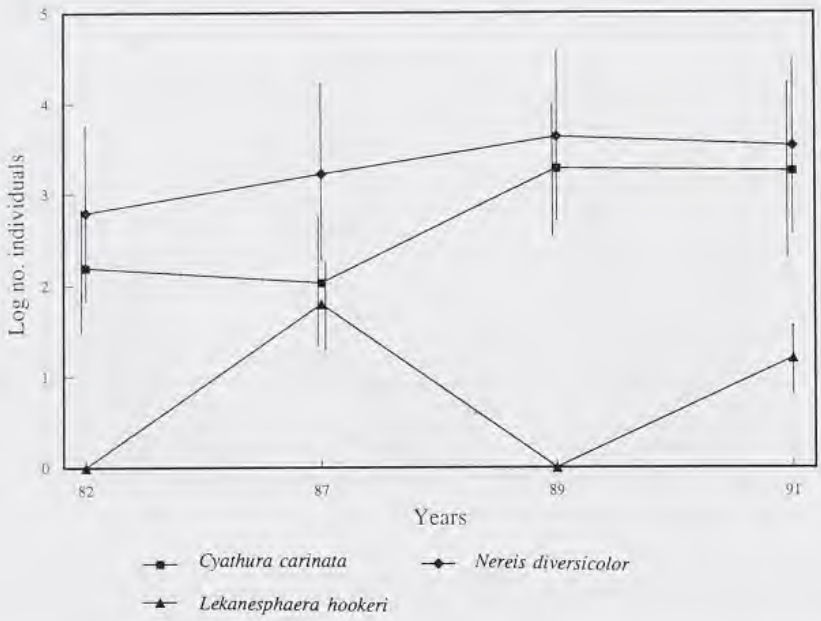



FIG. 7. — Changes in the abundance of dominants in sediments. ($log_{10}$, mean number of individuals.$m^2$ ± s.e.).

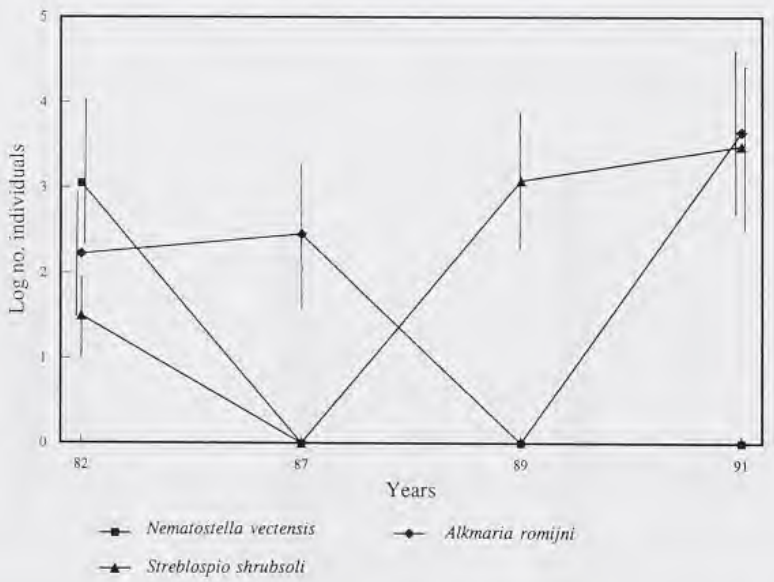



FIG. 8. — Changes in abundance of secondary species in sediments. ($log_{10}$, mean number of individuals $m^2$ ± s.e.).

The death of the aggregates of *F. enigmaticus* in 1987 may have contributed to several of the changes observed in the associated fauna. Most important amongst these was the demise of *C. insidiosum*. The other two abundant species, although they almost disappeared in 1987, were able to return to dominance in 1989.

The burrowing and mobile scavenging fauna which developed in 1987 evidently responded to the increased area available for occupation, created by the greater quantitiesof particulate material within the aggregates. Similar

Source : MNHN, Paris

changes were observed by RULLIER (1943), who found that *H. diversicolor* was present in abundance in recently dead aggregates. The accumulation of sediment may also have prevented some of the live aggregate species from occurring, such as *C. insidiosum*, although the quantity of sediment was never sufficient to eliminate all of the mobile amphipods. These species are still able to exploit the remaining space and utilise the high levels of suspended particulate material found in the water. As a consequence the dead aggregates are able to support a wider range of species than the live aggregates. Likewise the regenerating aggregates contain greater levels of sediment, principally in a central degenerated area, surrounded by an atoll of regenerating individuals. As a result the regenerating aggregates retain an equally diverse fauna.

The lack of sediment makes live aggregates unsuitable for burrowing species, but an additional factor reducing the diversity of the associated fauna could be competitive exclusion. KNIGHT–JONES & MOYSE (1961) have indicated that the growth form of *Filograna* aggregations optimises food utilisation, and *Ficopomatus* has somewhat similar spacing of individuals within the aggregates. The limited species numbers but large numbers of individuals found in live aggregates indicate that *L. pilosus, M. palmata* and *C. insidiosum* may have specific feeding requirements that do not conflict with that of *F.enigmaticus*. Between these species full exploitation of the available food resources may well occur, thus excluding other species. While conditions are stable the amphipod populations are likely to remain in balance with *F.enigmaticus*, maintaining themselves by larval brooding and direct settlement (LINCOLN, 1979).

The filter–feeding activity of *F. enigmaticus* is also likely to have an effect on the total energetics of the millpond. DAVIES *et al.* (1989) in a study of the Marina de Gama, near Cape Town, calculated that *F. enigmaticus* had the potential to reduce the particulate load of the water within the lagoon by 50 % each day. This ability to change the water quality has the potential to affect the fauna profoundly, within both the aggregates and the adjacent mudflats. The disappearance of live *F. enigmaticus* aggregates in 1987 corresponded with changes in the mudflat fauna, particularly a reduction in diversity. The remaining species, such as *H. diversicolor* and *L. hookeri*, mostly exhibited non–specialised feeding habits. These species were probably able to exploit the increased levels of suspended food that were not previously available to the sediment fauna. A further feature, related to the loss of the aggregates, was the substantial reduction in the numbers of *F. enigmaticus* larvae (THORP, 1994) which may have formed an important food source for some of the species with more specialised feeding habits. A good example of this is the polychaete *Eteone longa* (Fabricius, 1780), which FAUCHALD & JUMARS (1979) have indicated feeds specifically on other annelid larvae. With the reappearance of the live aggregates, and hence reduction in suspended food and an increase in larval numbers, it could be expected that the benthic species numbers in the sediment would increase. To some extent this situation has occurred, species numbers falling in the aggregates and increasing substantially in the sediment.

Considerable variation in the benthic fauna is evident, however, which cannot be explained wholly by the death of *F. enigmaticus*. Clearly other factors operate in the millpond which affect the benthic fauna and may have contributed to the demise of *F. enigmaticus*. Of principal importance amongst these is the intrusion of high salinity water. In 1982 the benthic fauna was composed of a range of species, that included several marine species, commonly occurring in Chichester Harbour; for example, *E. longa, Tharyx marioni* (de Saint–Joseph, 1894), *Manayunkia aestuarina* (Bourne, 1883) and *Cerastoderma edule* (L., 1758) (THOMAS, 1987). The disappearance of this group in 1987 and the appearance of several low salinity species, for example *Gammarus zaddachi* Sexton, 1912 and *Gammarus salinus* Spooner, 1947 suggests that a period of low salinity may have eliminated most of the marine species. THORP (1987) has indicated that protracted periods of low salinity occurred during the winter and spring of 1983–1987. The species most successful during this period were the typically euryhaline species, *H. diversicolor* and *Cyathura carinata*. The appearance of marine species in 1989 *Ascidiella aspersa* (O.F. Müller, 1771) and *Ciona intestinalis* (L., 1767) was localised in the vicinity of the tide gates where maximum salinities occur. This was followed in 1991 by the re–appearance of several species which clearly entered from Chichester Harbour; specifically *Ostrea edulis* L., 1758, *Eteone longa*, *Jassa falcata* (Montagu, 1880) and *Hydrobia ulvae* (Pennant, 1777). All of these species occurred in the year which followed a winter of almost constant high salinities, with zero salinity recorded only 15 % of the time.

These fluctuations in salinity, in combination with the biological effects due to the changes in health of the aggregates, have created a dynamic and unstable environment in the millpond. This is demonstrated by fluctuations in abundance of several of the benthic species, particularly *N. vectensis* and *A. romijni*, both of which are protected species in the U.K. These species, in keeping with many others that occupy extreme environments, can exploit to the maximum suitable conditions when they occur. Extreme conditions have also been cited by TEN HOVE (1979) as a factor in the development of mass occurrences of serpulids. These may be followed by dramatic declines, with, in the case of the serpulids, only the dead tubes to provide evidence of previous existence.

Source : MNHN, Paris

## ACKNOWLEDGMENTS

We would like to express our thanks to the following students; Clare WIMBLE, Carolyn ATKINS, John HOPKINS, Peter NICHOLLS and Ewen WILSON, for their valuable assistance with the collection of the faunal data. We would also like to express our gratitude to the trustees and members of the Slipper Millpond Preservation Society and Mrs Elizabeth KINLOCH for allowing the studies to take place. Particular thanks are also due to Mr. Bruce HAILSTONE for his unstinting assistance in the field.

## REFERENCES

BERTRAND, 1938. — Sur quelques Crustacés Malacostracés de la région Dinardaise. *Bull. Lab. Dinard*, **20** : 26–31.

DAVIES, B.R., STUART, V. & VILLIERS, de V., 1989. — The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus)* (Fauvel) and its effects on water quality in a coastal marina. *Est. Coastal Shelf Sci.*, **29** : 613–620.

EUZET, L. & PUJOL, M., 1963. — La faune associée à *Mercierella enigmatica* Fauvel (Annelida Serpulidae) dans quelques stations des environs de Sète. *Rapp. P.v. Comm. intern. Explor. scient. Méditerr.*, **17** : 833–842.

FAUVEL, P., 1933. — Histoire de la *Mercierella enigmatica* Fauvel Serpulien d'eau saumâtre. *Arch. Zool. exp. gén.*, **75** : 185–193.

FAUCHALD, K. & JUMARS, P.A., 1979. — The diet of worms: A study of polychaete feeding guilds. *Oceanogr. mar. Biol. Ann. Rev.*, **17** : 193–284.

FISCHER–PIETTE, E., 1925. — Sur la faune de la Rance et la présence de *Mercierella enigmatica* Fauvel. *Bull. Soc. Zool. France*, **50** : 347–350.

FISCHER–PIETTE, E., 1928. — Recherches de bionomie et d'océanographie littorale sur la Rance et le littoral de la Manche. *Ann. Inst. Océanogr.*, **5** : 310–311.

GOODHART, C.B., 1939. — Notes on the bionomics of the tube dwelling amphipod *Leptocheirus pilosus* (Zaddach). *J. mar. biol. Ass. U.K.*, **23** : 311–325. —

HOLME, N.A. & Mc.INTYRE, A.D., 1971. — *Methods for the study of the marine benthos*. Blackwell Scientific Publications, Oxford, 331 pp.

HOVE, H.A.ten., 1979. — Different causes of mass occurrence in serpulids, *In*: G. LARWOOD & B.R. ROSEN (eds), *Systematics Association Special* **11**, *Biology and Systematics of Colonial Organisms*. Academic Press, London and New York : 281–298.

KNIGHT–JONES, E.W. & MOYSE, J., 1961. — Intraspecific competition in sedentary marine animals. *Symp. Soc. exp. Biol.*, **15** : 72–95.

LINCOLN, R.J., 1979. — *British Marine Amphipods (Gammaridae)*. British Museum (Natural History). London., 657 pp.

RULLIER, F., 1943. — Observations sur *Mercierella enigmatica* Fauvel dans la Rance canalisée. *Bull. Lab. marit. Dinard*, **25** : 36–44.

SHEADER, M., 1978. — Distribution and reproductive biology of *Corophium insidiosum* (Amphipoda) on the north–east coast of England. *J. mar. biol. Ass. U.K.*, **58** : 585–596.

THOMAS, N.S., 1987. — *Aspects of the ecology of the macroinvertebrates in the intertidal soft sediments of Chichester Harbour*. Ph.D. Thesis, Portsmouth Polytechnic, 343 pp.

THORP, C.H., 1987. — Ecological studies on the serpulid polychaete *Ficopomatus enigmaticus* (Fauvel) in a brackish water millpond. *Porc. Newsl.*, **4** : 14–19.

THORP, C.H., 1994. — Population variation in *Ficopomatus enigmaticus* (Fauvel) (Polychaeta–Serpulidae) in a brackish water millpond, (1982–1992). *Mém. Mus. natn. Hist. nat.*, **162** : 585-591.

VUILLEMIN, S., 1965. — *Contribution à l'étude écologique du lac de Tunis. Biologie de* Mercierella enigmatica *Fauvel*. Thèse Doctorat d'Etat ès-Sciences Naturelles, Université de Paris, 554 pp.

Source : MNHN, Paris

# Population variation in *Ficopomatus enigmaticus* (Fauvel) (Polychaeta, Serpulidae) in a brackish water millpond at Emsworth, West Sussex, U.K.

*Clifford H. THORP*

Marine Laboratory, University of Porsmouth, School of Biological Sciences
Ferry Road, Hayling Island, Hampshire, PO11 0DG, U.K.

ABSTRACT

Since 1982 a population of *Ficopomatus enigmaticus* has been monitored with respect to larval settlement and tube accumulation on settlement panels. Prodigious settlements (1.3 x $10^7$.$m^{-2}$ max.) were recorded over the period 1982–85 and globular, reef–like aggregations increased in number on the muddy floor of the pond but, prior to the onset of breeding in 1986, the population `crashed' dramatically. While live adults were not observed in the years 1986–88 larval settlements continued, but with greatly reduced and decreasing maxima (1.6x$10^3$.$m^{-2}$, 1986; 1.1x$10^3$. $m^{-2}$, 1987 and 9.7 x $10^2$. $m^{-2}$, 1988). Since 1989 the adult population has recovered, being observed on the tide–gates and adjacent walls in particular (1989–90) and as small aggregates on the pond bottom (1991). The increase in the adult population has been reflected in in"reasing settlement densities (2.8 x $10^5$. $m^{-2}$, 1989 to 2.5 x $10^6$. $m^{-2}$, 1991). Evidence is offered to explain the population "crash" of 1986 and it is suggested that it resulted from the age of the adult population and a lack of both overwintering reserves and recruitment. It is also suggested that serpulid polychaetes which exhibit population "explosions", such as *F. enigmaticus*, are equally likely to suffer population "crashes" and, further, that population numbers may well fluctuate in a cyclical manner.

RÉSUMÉ

**Variation de la population de *Ficopomatus enigmaticus* (Fauvel) (Polychaeta, Serpulidae) dans une retenue d'eau saumâtre à Emsworth, West Sussex, RU.**

Depuis 1982, une étude, concernant l'établissement de larves et l'accumulation de tubes sur les panneaux expérimentaux, a été menée sur une population de *Ficopomatus enigmaticus*. De 1982 à 1985, des fixations considérables ont été enregistrées et des agrégats de forme sphérique semblables à des récifs augmentèrent en nombre sur le fond vaseux du bassin de retenue. Cependant, la population s'effondra de façon drastique et ceci avant le début de la période de développement de 1986. Alors qu'aucun adulte vivant ne fut observé de 1986 à 1988, la fixation de larves continuait mais leur abondance était extrêmement réduite et continuait à decroître (1.6 x $10^3$.$m^{-2}$ en 1986; 1.1 x $10^3$. $m^{-2}$ en 1987 et 9.7 x $10^2$. $m^{-2}$ en 1988). Depuis 1989, la population adulte s'est rétablie et elle fut observée sur les portes des marées et sur les parois adjacentes, tout particulièrement en 1989 et 1990. En 1991, de petites agrégats s'établirent au fond du bassin de retenue. L'augmentation de la population adulte est le reflet de cette densité d'établissement larvaire (2.8 x $10^5$. $m^{-2}$ en 1989 à 2.5 x $10^6$. $m^{-2}$ en 1991). Quelques hypothèses sont

---

THORP, C.H., 1994. — Population variation in *Ficopomatus enigmaticus* (Fauvel) (Polychaeta-Serpulidae), in a brackish water millpond at Emworth, West Sussex, U.K. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 585-591. Paris ISBN 2-85653-214-4

Source : MNHN, Paris

avancées afin d'expliquer l'effondrement de la population de 1986. Il est suggéré qu'elle fut causée par l'âge de la population adulte, et par l'absence de réserves hivernales ainsi que par l'absence de recrutement. Il est aussi suggéré que les serpules qui, comme les *F. enigmaticus*, connaissent des explosions de leurs populations, pourraient de la même façon, subir un effondrement drastique de celles-ci. De surcroît, il se pourrait que ces populations fluctuent de façon cyclique.

## INTRODUCTION

The serpulid *Ficopomatus enigmaticus* (Fauvel), first reported in Britain from the London Docks in 1921 (MONRO, 1924), has been recorded from a number of brackish water sites, mostly confined to southern coasts (ZIBROWIUS & THORP, 1989). Although transitory populations have been recorded from Danish waters, (WESENBURG–LUND, 1941; HARTMANN–SCHRÖDER, 1971), and a population sustained by heated power station effluent (RASMUSSEN, 1958), *F. enigmaticus* is considered to reach its northern limit of reproduction on British coasts, several records again being associated with warm water effluents (NAYLOR, 1959; MARKOWSKI, 1962). *F. enigmaticus* was first recorded from Chichester Harbour, West Sussex, in 1974 (THORP, 1980) and since 1980/81 has flourished in the brackish water millpond of the now defunct Slipper tidemill at Emsworth, West Sussex (50°50.5'N, 0°56'W). The millpond has a surface area of 2.7 ha and, apart from a meandering deeper water channel, has a maximum depth < 1.5 m (THORP, 1987). Seawater enters from the adjacent Chichester Harbour through tide–gates at the south end during spring tides > 4.3 m while fresh water enters from the north as part of the River Ems. A relatively constant water level is maintained within the pond during low tide periods by the tide–gates (THORP, 1987). Within the pond limited hard substrata are readily "colonised" by *F. enigmaticus*, from the tide–gates and adjacent brick walls to the stems of fringing reeds, but the most characteristic growths are globular mini–reefs (aggregates). The aggregates, apparently resting on the soft mud substratum in depths of 0.75–1.0 m (cf. RULLIER, 1943), have resulted from larval settlement on small solid objects such as pebbles, stones, cans, bottles, etc.

Since May 1982 water temperature, salinity and *F. enigmaticus* settlement have been monitored weekly. Temperature and salinity are very variable and, despite the shallowness of the ponds, exhibit frequent and marked discontinuities between the surface and the pond bottom at 0.75–1.0 m (THORP, 1987). The overall salinity regime (0.3–34.1 P.S.U.) of the bottom waters, where greatest growth of the aggregates occurs, is both lower and more variable in winter/spring than in summer/autumn (THORP, 1987). The overall pattern of salinity variation is of high salinity over spring tide and low salinity over neap tide periods. Apart from when the River Ems is in spate, spring tide salinities are gradually reduced over the neap tide period with an abrupt return to high salinity at the next springs. The temperature range of the bottom waters also varies, from 5.5–30 °C in the warmer months of the year (May–October) to –1–20 °C (November–April). Larval settlement is confined to the period May to October/November, when the minimum bottom water temperature is > 10°C, and exhibits a marked lunar periodicity with settlement occurring over the neap tides (THORP, 1987 and unpublished data). Maximum settlements have exceeded $10 \times 10^6$. $m^{-2}$ (THORP, 1987). In water temperatures > 10 °C spawning is apparently initiated (triggered) by an influx of higher salinity water (spring tides). The minimum salinity required has not been determined and spawning can be delayed in the absence of adequate phytoplankton levels (THORP, 1987).

Although there are many records of the incidence of *Ficopomatus* spp., several giving data for a few years (TEBBLE, 1953; HILL, 1967; STRAUGHAN, 1972) and/or detailed seasonal data (HILL, 1967; STRAUGHAN, 1972; DIXON, 1981), continuous observations of a single population over a long period are lacking. The present paper, therefore, presents some results from monitoring a population of *F. enigmaticus* over the period 1982–92 and suggests reasons to explain the pattern of variation.

## MATERIALS AND METHODS

Panel studies employed 25 x 25x 0.6 cm "Tufnol" panels attached horizontally to a frame, constructed from 1.8 cm "Durapipe". The panels were held 15cm above the pond bottom at 0.75–1.0 m depth. Settlement was assessed using weekly (6–8 days) panels while seasonal panels were used to assess tube accumulation (weight). Settlement density was determined using a 10 x 10 cm grid within a 2 cm wooden frame. Light settlements were scored by placing the grid in each of the four corners of the panel and counting the total number of worms within the10 x 10 cm grid area under a binocular microscope. Progressively heavier settlements were scored using random numbers to select 10 1 x 1 cm squares within each grid and/or using a squared eyepiece grid within the

Source : MNHN, Paris

1 x 1 cm squares. Mean values were expressed as numbers/m$^2$. Seasonal panels were weighed weekly on a spring balance after standard drainage and removal of silt, attached algae and crabs.

## RESULTS

SEASONAL SETTLEMENT. — Figure 1 presents weekly settlement data for the years 1982–1992. Settlement begins in mid to late May and ends in late October/November. The overall pattern demonstrates a series of peaks and troughs which result from settlement occurring over neap tides (THORP, 1987 and unpublished data). The lack of precision in figure.1 reflects that weekly sampling was dictated by teaching commitments rather than a precise relation to the tidal phases. Thus, panel changing in the course of a set of neap tides could result in consecutive panels attracting heavy settlements. The 10–year period can be split into three phases. Firstly 1982–85, which saw a prolonged period of high settlements, several > 1x $10^6$. m$^{-2}$ and some > 10 x $10^6$. m$^{-2}$. This prolific phase was followed by greatly reduced settlements from 1986–88. In early March 1986 the population suffered a catastrophic

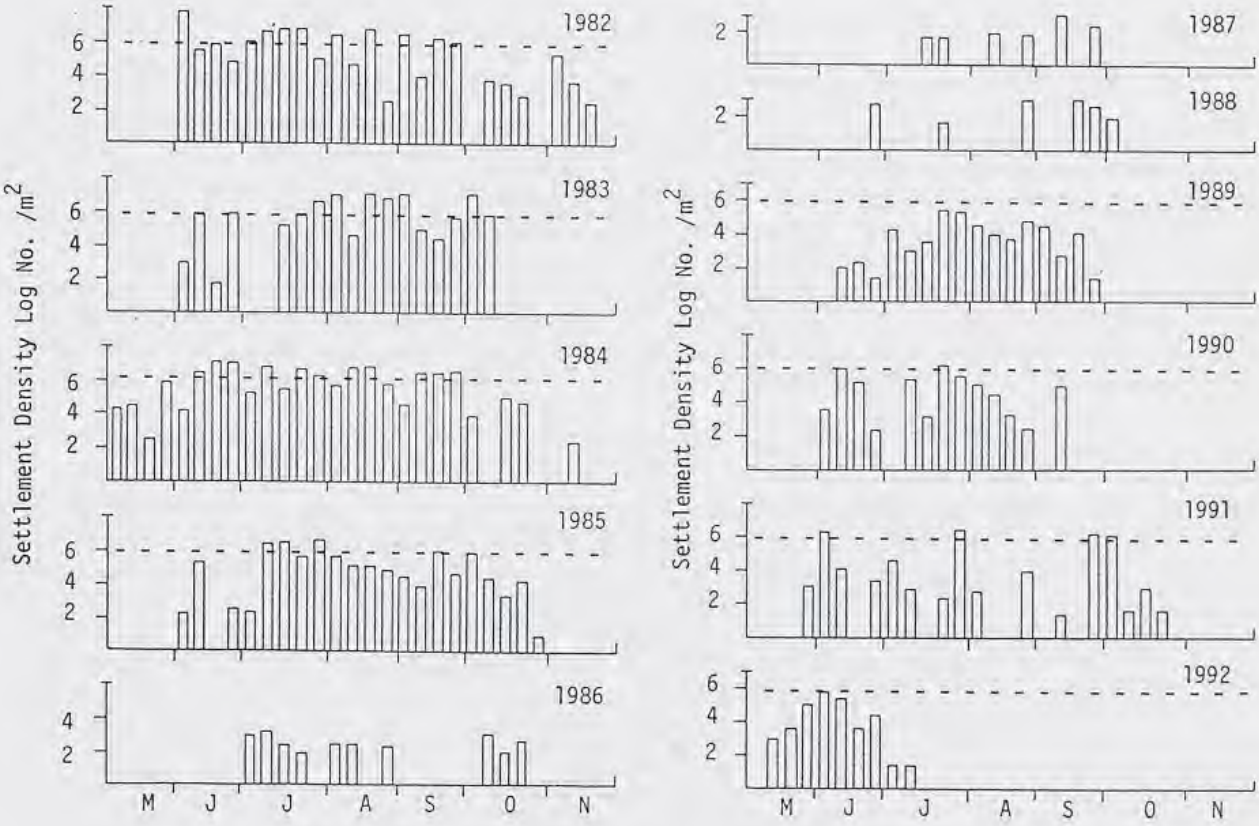



FIG. 1. — Settlement density of *F. enigmaticus* on weekly settlement panels, 1982–92.

"crash"; all aggregates died and live adults were not observed within the pond. Despite the apparent lack of live adults, small settlements (max. 1600 m$^{-2}$) occurred during shortened settlement seasons. The third phase, 1989–91, witnessed an increase in both the length of the settlement season and settlement density, settlements > 1 x $10^6$. m$^{-2}$ being recorded in both 1990 and 1991. Live adults again became abundant on the tide–gates and adjacent brick walls and, in 1991, small irregular aggregates were observed on the muddy pond bottom. The 1992 season began well, with promising settlements in May and June. Late June, however, witnessed very extensive and dense (80–90 % cover) growth of the green alga *Ulva lactuca* on the pond bottom and July saw a dramatic

Source : MNHN, Paris

reduction in settlement. Throughout August and September the pond was allowed to flush tidally to give low–tide access for repairs to a road bridge which crosses the pond and no further settlements were recorded. The 10–year period, therefore, exhibits a cyclical pattern of initial abundance followed by a dramatic decline and subsequent recovery.

TUBE ACCUMULATION. — Table 1 demonstrates considerable variation in the weight of worms (+ tubes) accumulating on weekly panels which does not appear to be related to settlement density. Increase in weight of

TABLE 1. — Tube accumulation (g dry weight) of *F. enigmaticus* on weekly panels.

| Immersion Date | Settlemennt ($x10^6$. $m^{-2}$) | Dry weight of tubes | Weight Increase (/day) |
|---|---|---|---|
| 13-21.06.84 | 12.1 | 3.24 | 0.40 |
| 21-27.06.84 | 10.6 | 2.57 | 0.43 |
| 04-12.07.84 | 8.5 | 8.76 | 1.09 |
| 20-27.07.84 | 5.5 | 1.11 | 0.16 |
| 10-16.08.84 | 6.3 | 1.58 | 0.26 |
| 16-23.08.84 | 8.7 | 6.84 | 0.98 |

seasonal panels also fails to reveal any trend (Table 2). There is again no apparent relationship between weight increase and initial settlement density in the long term although, in 1983, the later panel (12.8.83) initially increased in weight more rapidly which may reflect the greater settlement density. This, however, is not supported by the different initial settlements in 1984. In both 1983 and 1984 the initial low settlements were probably augmented by much greater settlements within three weeks (Table 2).

The explosive increase of *F. enigmaticus* in 1982/83 encouraged a considerable increase in the number of shore crabs (*Carcinus maenas L.*) within the pond which resulted in predatory damage to both the naturally–occurring aggregates and those on the panels, seriously affecting the late season accumulation.

## DISCUSSION

SEASONAL SETTLEMENT. — Settlement is confined to summer/autumn when the minimum bottom temperature is > 10 °C (THORP, 1987) which contrasts with a minimum of 18 °C in the Thames Estuary (DIXON, 1981). In the first four years (1982–85) prodigious settlements occurred but it is possible to observe the onset of the 1986–88 decline during 1985. In that year only three weekly panels attracted more than 1 x $10^6$. $m^{-2}$ in contrast to 9, 6 and 11 panels in the previous three years respectively. The cause of the reduced settlements can be deduced from the physical conditions prevailing throughout summer/autumn 1985. Through April, and particularly May, 1985 little or no sunshine prevented any phytoplankton increase. Strong sunshine in the last week of May, however, resulted in a rapid increase in visible phytoplankton levels which probably triggered spawning, with small settlements in the first two weeks of June. This was followed by settlements > 2 x $10^6$. $m^{-2}$ in July and a subsequent decline until late September. The sunny period of late May/early June was followed by a long period of poor summer weather during which pond water clarity suggested very low phytoplankton levels. In mid–September 2–3 weeks of better weather promoted a small plankton increase. As the bottom water temperature was > 10 °C throughout this period it is probable that the decline in settlement can be attributed to low phytoplankton levels. The "events" of the 1985 summer most probably led, at least in part, to the catastrophic decline of the adult population in March 1986. Overwintering adults withdraw to the lowermost levels of their tubes during cold winters and assume a state of torpor (ZIBROWIUS & THORP, 1989). Consequently, organic and inorganic debris settling from the water column accumulate within upward–facing tubes and must be cleared before normal activity can be resumed. That this does not always happen is inferred from aggregates where the central area, containing the upward–facing tubes, dies out leaving the more oblique and lateral–facing tubes to form atoll–like structures. It is probable that, with winter inactivity and zero phytoplankton levels, *F. enigmaticus* has to overwinter on reserves built up over the previous summer/autumn. The low phytoplankton levels through 1985 could have resulted in reduced somatic reserves for overwintering, causing weakened animals, unable to clear their tubes, to perish. KNIGHT–JONES & MOYSE (1961) reported that gregarious animals can assume a growth form to maximise their feeding potential, and it is this

Source : MNHN, Paris

strategy which results in *F. enigmaticus* tubes being evenly spaced and their feeding apparatus (branchial crown) deployed to its best advantage. In practice the branchial crowns of adjacent animals are contiguous, largely preventing the settlement of larvae or sediment within the aggregates. While the longevity of *F. enigmaticus* remains unclear it is possible that by 1986 the aggregates comprised animals which were 4–5 years old. This is based on the likelihood that there is little or no secondary settlement as long as the aggregates maintain their integrity and also, that the limited hard substrata within the pond complex were rapidly occupied. Thus "old age" and a lack of overwintering reserves could have resulted in debility which led to the massive mortality.

TABLE 2. — Tube accumulation (Kg wet weight) of *F. enigmaticus* on nseasonal panels. Is: Initial settlement density. Is+3: Additional settlements withing 3 Is. c : Crab predation of tubes.

| Immersion Date | Weeks Immersion | | | | | | Max. Wt | Is ($10^6$. $m^{-2}$) | Is+3 ($10^6$. $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| | 2 | 4 | 9 | 10 | 12 | 15 | | | |
| 14.07.83 | | 1.2 | 4.8 | 6.3 | 7.5 | 9.3c | 9.4 | 0.81 | 2.1/9.6 |
| 12.08.83 | | 2.2 | 5.0 | 5.1 | 5.1c | | 5.2 | 11.97 | 7.1/13.4 |
| 17.05.84 | | | 2.4 | 3.2 | 4.5c | 5.4 | 5.4 | 0.94 | 3.3 |
| 27.06.84 | | 1.2 | 3.3 | 3.4c | 3.5 | 3.6 | 3.7 | 0.21 | 8.5/13.5 |
| 27.07.84 | 0.5 | 1.0 | 1.8 | | 1.5c | | 1.8 | 2.12 | 6.3/8.2 |
| 05.06.85 | | 0.5 | | 1.2 | 1.9 | 2.3c | 2.6 | 0.15 | - |
| 07.06.90 | | 0.5 | 2.5 | 3.0 | 3.4c | 3.2 | 3.4 | 0.18 | 0.2 |
| 09.07.91 | | | 1.2 | 1.4 | 1.5c | 1.5 | 1.5 | 2.54 | - |
| 08.05.92 | | 0.5 | 0.6 | | | | | 0.11 | 0.59 |

Through 1986–88 a few adults must have survived to provide the small settlements observed, but these years were also notable for low phytoplankton levels. The years 1989–91 not only witnessed very hot and prolonged summers, particularly 1989, but also increased and extended phytoplankton "blooms". Consequently, not only did the breeding season of *F. enigmaticus* increase in length, but maximum settlements increased, with four weekly counts > 1 x $10^6$. $m^{-2}$ in 1991.

It was expected that 1992 might witness a population explosion. Thick and prolonged ice–cover in February 1991, while it may have caused considerable mortality in the adult population, crushed the remaining "dead" aggregates freeing additional hard substrata. After good settlements in mid–May, which accompanied high phytoplankton levels, settlement declined markedly in July. While this failure can be associated with a 'crash' in the phytoplankton level it can not be related to reduced sunshine levels. It does, however, appear to be associated with the very heavy growth of *Ulva lactuca* which developed on the bottom of the pond from early June. HIMMELMANN (1980) reported the significance of phytoplankton levels in the synchronisation of spawning in marine invertebrates and, while the *Ulva* undoubtably `blanketed' the existing aggregates its true effect probably was to greatly reduce the nutrients available to sustain the phytoplankton and consequently remove an essential spawning trigger. While *Ulva* featured in the millpond as shortlived, dense growths in previous years, notably 1991 (THORP, unpublished data), it was the density and prolonged nature of the 1992 growth that was significant. With 1992 being the fourth 'dry' year in succession in Britain the fresh water flow from the River Ems has been greatly reduced bothnaturally and through increased abstraction by the local water authority. Consequently the weekly bottom water salinity only fell below 20 twice in 1992 (Jan/July). Seawater entering the millpond is probably high in dissolved nutrients, as a result of the high sewage effluent loading of the adjacent and connected Langstone Harbour (Portsmouth Polytechnic, 1976). THOMAS (1987) also referred to localised increases in organic pollution in Chichester Harbour arising from both small sewage discharges and land drainage from the surrounding agricultural land. Not only do point discharges occur in the area of the harbour adjacent to the millpond but the River Ems also drains a considerable area of farmland. Thus *Ulva*, which grows prolifically in Langstone Harbour, has been able to flourish in relatively high salinity, warm, nutrient–rich water at the expense of possibly brackish water phytoplankton species.

TUBE ACCUMULATION. — Mass formation of serpulids has been variously attributed to a complex of environmental factors including competition for space and food; reduced predation; gregarious behaviour; larval retention; primary productivity and hydrographic factors such as temperature and salinity (SCHROEDER &

Source : MNHN, Paris

HERMANS, 1975; BOSENCE, 1979; HOVE, 1979). Significantly HOVE (1979) also stated that decreased competition with other animals, mainly for space, may lead to massive numbers in species at the periphery of their ranges. In optimum conditions the millpond embraces all these factors, acting as a brackish lagoon and experiencing elevated temperatures, limited substrate availability and high primary productivity. The tide–gate control of water level will encourage larval retention and there are no major competitors for space or food. It is rather the success of *F. enigmaticus* which creates the problems.

While the length of settlement season is governed by temperature, tube accumulation within seasons may be affected by both food availability and initial settlement density. Tube accumulation in both 1983 and 1984 can be related to the length of the immersion period (Table 2) and there appears to be some support for the idea that initial settlement density is involved within years, cf. 14/7 and 12/8 in 1983 particularly at 9 weeks. Similar data for 1984 (15/5 and 27/6), however, more likely reflects the high subsequent settlements on the 27/6 panel. In the absence of phytoplankton data it is difficult to comment on the effect of food level, although the 1985 panel (5/6) suggests a strong connection. While the low rate of accumulation in 1985 may reflect the small initial settlement ($1.5 \times 10^5$. $m^{-2}$) when compared to the 1990 panel (7/6), it may well result from the low phytoplankton levels observed in 1985. Heavy metal levels in Chichester Harbour will be very low (THOMAS, 1987) and unlikely to have any deleterious effect. Although there are >8,000 small boats (98.7% < 12 m in length) moored or berthed in marinas in the harbour, as 74 % (2,115 ha) of the total harbour area (2,849 ha) is intertidal (Chichester Harbour Conservancy, pers.comm), it is probable that tidal flushing greatly reduced any effects of organo–tins prior to the ban on their general use in antifouling paints in 1987.

The overall pattern, of population proliferation followed in turn by a catastrophic decline and subsequent recovery, possibly represents the normal pattern in a species with great fecundity, relative longevity and occupying a habitat with limited available substrata. Indeed BOSENCE (1979) stressed the importance of limited substrata in the rapid build–up of tube aggregates in *Serpula vermicularis*. Massive settlement of *F. enigmaticus* would quickly occupy all available hard substrata within perhaps one or two seasons and the close packing and disposition of the tubes would prevent significant recruitment and lead to an ageing population prone to disaster. It is suggested that disaster struck due to a lack of overwintering reserves resulting from the poor summer of 1985. Thus, gregarious species with an epidemic spawning capacity could be expected to exhibit an alternating pattern of success and decline. In this respect it is interesting to note that the invasive serpulid, *Hydroides ezoensis* Okuda, exhibited a similar, if partial, population decline in Southampton Docks in 1987/88. *H. ezoensis*, first recorded as a single specimen from the intake channel of Fawley Power Station, Southampton Water, in 1977, formed massive encrustations (30cm thick) in the intertidal region of most dock structures (THORP *et al.*, 1987). The population on the Town Quay, however, died and sloughed off in 1988/89, this event preceding demolition and reconstruction of the quay (THORP, unpublished data).

KEENE (1980) and DAVIES *et al.* (1989) both reported an apparent beneficial interrelationship between populations of *F. enigmaticus* and sediment and nutrient levels within semi–enclosed waters. Circumstantial evidence from the present study suggests a similar relationship within the Slipper pond where high phytoplankton levels complement high settlement densities. While it is truly a "chicken and egg" situation as to which comes first, elsewhere it has been shown that the overall economy of the pond can be related to the success of *F. enigmaticus* (THOMAS & THORP, 1994).

## ACKNOWLEDGEMENTS

I am happy to acknowledge the kindness that the trustees and members of the Slipper Millpond Preservation Association have extended towards me in allowing me to work in the pond. I am also indebted to Havant Borough Council, and particularly Alistair MARTIN, for making the Hayling Island, Beachlands, meteorological records available to me. I also acknowledge the assistance of James HEPBURN in making this a more complete record by covering some of my absences.

## REFERENCES

BOSENCE, D.W.J., 1979. — The factors leading to aggregation and reef formation in *Serpula vermicularis* L. *In:* G. LARWOOD & B.R. ROSEN (eds), *Systematics Association Special Volume No. 11, Biology and Systematics of Colonial Organisms*. Academic Press, London and New York : 299-318.

DAVIES, B.R., STUART, V. & VILLIERS, de V., 1989. — The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* Fauvel) and its effects on water quality in a coastal marina. *Est. Coastal Shelf Sci.*, **29** : 613–620.

Source : MNHN, Paris

DIXON, D.R. 1981. — Reproductive biology of the serpulid *Ficopomatus (Mercierella) enigmaticus* in the Thames Estuary, S.E. England. *J. mar. biol. Ass. U.K.*, **61** : 805–815.

HARTMANN–SCHRÖEDER, G., 1971. — Zur Unterscheidung von *Neopomatus* Pillai und *Mercierella* Fauvel (Serpulidae, Polychaeta). (Mitt neuen Beiträgen zur Kenntnis der Ökölogie und der Röhrenform von *Mercierella enigmatica*). *Mitt. hamb. zool. Mus. Inst.*, **67** : 7–27.

HILL, M.B., 1967. — The life cycles and salinity tolerance of the serpulids *Mercierella enigmatica* Fauvel and *Hydroides uncinata* (Philippi) at Lagos, Nigeria. *J. Anim. Ecol.*, **36** : 303–321.

HIMMELMAN, J.H., 1980. — Synchronisation of spawning in marine invertebrates by phytoplankton. *In:* W.H. CLARKE Jr & T.S. ADAMS (eds), *Invertebrate Reproduction, Developments in Endocrinology*. Elsevier, North Holland, Amsterdam : 3-19.

HOVE, H.A. ten., 1979. — Different causes of mass occurrence in serpulids. *In:* G. LARWOOD & B.R. ROSEN (eds), *Systematics Association Special Volume No. 11, Biology and Systematics of Colonial Organisms*. Academic Press, London and New York : 281-298.

KEENE, Jr., W.C., 1980. — The importance of a reef–forming polychaete, *Mercierella enigmatica* Fauvel, in the oxygen and nutrient dynamics of a hypereutrophic subtropical lagoon. *Est. Coastal Shelf Sci.*, **11** : 167–178.

KNIGHT–JONES, E.W. & MOYSE, J., 1961. — Intraspecific competition in sedentary marine animals. *Symp. Soc. exp. Biol.*, **15** : 72–95.

MARKOWSKI, S., 1962. — Faunistic and ecological investigations in Cavendish Dock, Barrow–in–Furness. *J. Anim. Ecol.*, **31** : 42–52.

MONRO, C.C.A., 1924. — A serpulid polychaete from London Docks (*Mercierella enigmatica*, Fauvel). *Ann. Mag. nat. Hist.*, (9) **13** : 155–159.

NAYLOR, E., 1959. — The fauna of a warm dock. *Proc. XVth intern. Congr. Zool.*, London 1958 : 259–262.

PORTSMOUTH POLYTECHNIC, 1976. — *Langstone Harbour Study -The effect of sewage effluent on the ecology of the harbour.* Portsmouth Polytechnic. Report to the Southern Water Authority, 365 pp.

RASMUSSEN, E., 1958. — Emigranter.1. Kobenhavns Sydhavn. *Naturens Werden.*, **8** : 231–234 and 246–248.

RULLIER, F., 1943.— Observations sur *Mercierella enigmatica* Fauvel dans la Rance canalisée. *Bull. Lab marit. Dinard*, **25** : 36–44.

SCHROEDER, P.C. & HERMANS, C.O., 1975. — Annelida : Polychaeta. *In:* A.C. GIESE & J.S. PEARSE (eds), *Reproduction of Marine Invertebrates, 3. Annelids and Echiurans*. Academic Press, New York and London : 1-213.

STRAUGHAN, D., 1972. — Ecological studies of *Mercierella enigmatica* Fauvel (Annelida: Polychaeta) in the Brisbane River. *J. Anim. Ecol.*, **41**: 93–135.

TEBBLE, N., 1953. — A source of danger to harbour structures – encrustation by a tubed marine worm. *J. Inst. munic. Engin.*, **80** : 259–265.

THOMAS, N.S., 1987.— *Aspects of the ecology of the macroinvertebrates in the intertidal soft sediments of Chichester Harbour*. Ph. D Thesis, Portsmouth Polytechnic, 343 pp.

THOMAS, N.S. & THORP, C.H., 1994. — Cyclical changes in the fauna associated with tube aggregates of *Ficopomatus enigmaticus* (Fauvel). *Mém. Mus. Nat. Hist. nat. Zoologie.*, **162** : 571-580.

THORP, C.H., 1980. — The benthos of the Solent. *In: The Solent Estuarine System: an assessment of present knowledge*. Natural Environment Research Council Publication, London (C) **22** : 76–85.

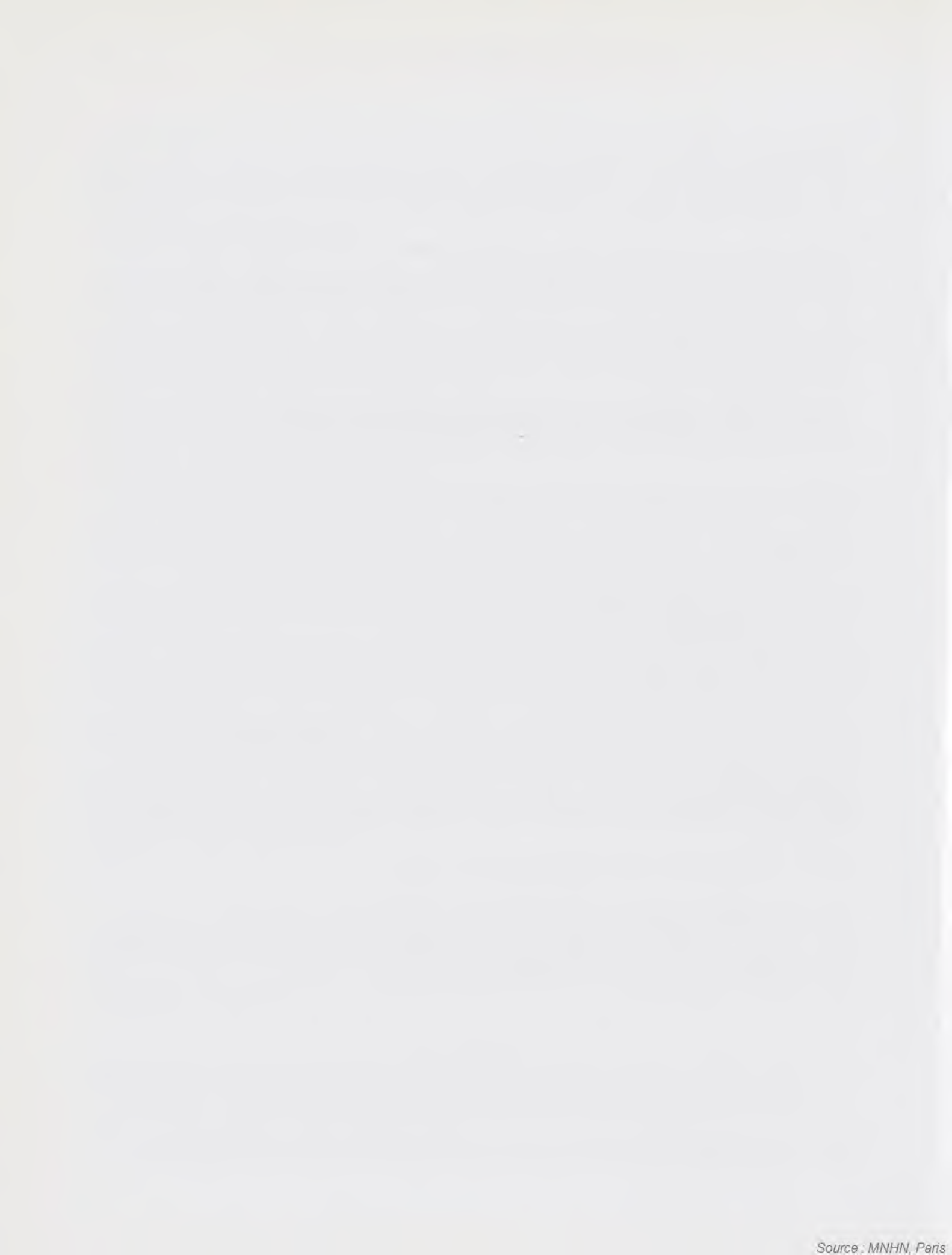
THORP, C.H., 1987. — Ecological studies on the serpulid polychaete *Ficopomatus enigmaticus* (Fauvel) in a brackish water millpond. *Porc. Newsl.*, **4** : 14–19.

THORP, C.H., PYNE, S. and WEST, S.A., 1987. — *Hydroides ezoensis* Okuda, a fouling serpulid new to British coastal waters. *J. nat. Hist.*, **21** : 863–877.

WESENBERG–LUND, E., 1941. — Notes on Polychaeta I. 1. *Harmothoe bathydomus* Hj.Ditlevsen refound. 2. On the sabellid genus *Fabricus*. 3. Three polychaetes from Ringkjobing Fjord, unrecorded in Denmark. 4. *Mercierella enigmatica* Fauvel, a serpulid new to Denmark. *Vidensk. Medd. Dansk. Nat. Foren. Kobenhavn.* **105** : 31–47.

ZIBROWIUS, H. & THORP, C.H., 1989. — A review of the alien serpulid and spirorbid polychaetes in the British Isles. *Cah. Biol. mar.*, **30** : 271–285.

Source : MNHN, Paris



Source : MNHN, Paris

# Polychaetes of commercial and applied interest in Italy: an overview

*M. Christina GAMBI*, Alberto CASTELLI°°, Adriana GIANGRANDE***, P. LANERA****, Daniela PREVEDELLI** & R. ZUNARELLI VANDINI***

* Laboratorio di Ecologia del Benthos-Stazione Zoologica "Anton Dohrn", Ischia, Napoli, Italy
°° Dipartimento di Scienze Antropologiche, Università di Sassari, Italy
** Dipartimento di Biologia Animale, Università di Modena, via dell'Università 4, Modena, Italy
*** Dipartimento di Biologia, Università di Lecce, via Monteroni di Lecce, Lecce, Italy
****Bioservice Soc. Coop., vico San Domenico Maggiore 9, Napoli, Italy

## ABSTRACT

The commercial interest of polychaetes is mainly due to their use as bait in recreational fishing and as food in aquaculture. The species of worms collected in Italy for these commercial and applied purposes is reviewed. Eight species of worms are collected for bait in Italian waters. *Hediste diversicolor*, *Perinereis cultrifera*, *Perinereis rullieri* and *Marphysa sanguinea* are collected from the Venice Lagoon. *Lumbrineris impatiens* is harvested in the Gulf of Naples, while *Diopatra cuprea cuprea* is collected from a littoral lagoon in Southern Sardinia and *Sabella spallanzanii* from other coastal areas of Sardinia. Finally, *Eunice aphroditois* is collected along the coasts of Apulia. A review of the literature on the effects of worm exploitation on the population, the associated communities and the environment, pointed out different results and patterns, and suggested the need for further studies and for legislation to control indiscriminant bait collecting to ensure a balance between the environment and the polychaete resource. Moreover, for the species that are imported from Korea, Japan, U.S.A. and other European countries, there is a risk of their accidental introduction into local biotopes. In this study we show that small-sized, "r-strategist" polychaetes, such as *Spio decoratus* or *Polydora ciliata*, are suitable food for juveniles of fish and crustaceans in aquaculture.

## RÉSUMÉ

**Les Polychètes d'intérêt commercial et appliqué en Italie : une revue**

Les Annélides Polychètes sont devenus un marché important car ils sont de plus en plus utilisés comme appât pour la pêche "au gros" et comme nourriture en vue de l'élevage dans des fermes aquatiques. Cette étude est l'actualisation de ce que nous savons en Italie sur l'utilisation des vers dans ces buts commerciaux. Huit espèces de polychètes sont utilisées comme appât dans les eaux italiennes. *Hediste diversicolor*, *Perinereis cultrifera*, *Perinereis rullieri* et *Marphysa sanguinea* sont pêchés dans la lagune de Venise. *Lumbrineris impatiens* est capturé par des plongeurs professionnels dans le golfe de Naples, alors que *Diopatra cuprea cuprea* et *Sabella spallanzanii* se pêchent dans les zones littorales de la

GAMBI, M.C., CASTELLI, A., GIANGRANDE, A., LANERA, P., PREVEDELLI, D. & R. ZUNARELLI VANDINI, 1994. — Polychaetes of commercial and applied interest in Italy: an overview. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 593-603. Paris ISBN 2-85653-214-4

Source : MNHN, Paris

Sardaigne. L'espèce *Eunice aphroditois* est pêchée par des marins professionnels et des pêcheurs "au gros" le long de la côte des Pouilles. Les études effectuées à ce jour sur les effets de la pêche des vers sur le niveau des populations, sur les communautés associées et le biotope ont conduit à des résultats qui suggèrent la nécessité d'autres recherches et d'une législation adéquate pour assurer un équilibre entre l'environnement et cette ressource en Polychètes. Comme beaucoup d'autres espèces étrangères sont importées des Etats-Unis, de la Corée, du Japon et d'autres pays européens, il reste aussi le risque de leur introduction accidentelle dans les biotopes locaux. Dans cette étude on montre également que des espèces de Polychètes de petites dimensions et à stratégie "r", comme *Spio decoratus* ou *Polydora ciliata*, peuvent servir de nourriture complémentaire à de jeunes poissons et de jeunes crustacés élevés dans un but commercial.

## INTRODUCTION

Polychaetous annelids are gaining significant commercial importance because they are increasingly used as bait for amateur and professional fishing. The widespread and ancient activity of worm collecting for angling is relatively well documented but quantified only in a few cases, mainly along the North American coasts (D'ASARO & CHEN, 1976; CREASER *et al.*, 1983), in East Asia (CHOI, 1985) and in Northern Europe (BLAKE, 1979a, b; HEILIGENBERG, 1982; OLIVE, 1994 a). The commercial value of the most exploited species have been documented by various authors (KLAWE & DICKIE, 1957; CREASER *et al.*, 1983; SARDA, 1989; CHEN, 1990). Recently OLIVE (in press) summarized the different patterns of worm exploitation and the potential for their aquaculture-based production. In most countries, including Italy, species are harvested from field populations (KLAWE & DICKIE, 1957; BLAKE, 1979a, b; CHOI, 1985), and only a few cases of commercial rearing are known (RYTHER *et al.*, 1975; KURIHARA, 1983; OLIVE, 1994).

Polychaetes are also used for other applied purposes, such as food in mariculture, decomposers of domestic and aquaculture organic wastes (TENORE & GOPALAN, 1974; TENORE *et al.*, 1974; RYTHER *et al.*, 1975) and test animals for toxicological studies (REISH, 1980). The aim of this study is to review the species of polychaetes that are harvested as bait, or have a potential applied interest in Italy, and describe their known biology and their methods of harvesting.

## RESULTS

Eight species of polychaetes are commercially collected from natural populations in Italy. The sites of more intensive harvesting for each of these species are shown in figure 1. Species are generally dug from tidal flats or from lagoons and shallow littoral biotopes by professional and amateur fishermen who use special raking hoes or shovels. A few species are harvested by SCUBA divers by hand or with small shovels in shallow waters from soft or hard substrates (GAMBI *et al.*, 1992; BELLO, 1993). Data on number of diggers and on quantity of specimens collected, their seasonality and commercial value are largely unavailable from the commercial companies involved in this market which is only just developing in Italy.

***Hediste diversicolor*** (O.F. Müller, 1778).

This euryhaline species is common in various Italian brackish zones (GIANGRANDE *et al.*, 1983-84), and it is commercially harvested mainly from the Venice Lagoon (Fig. 1). Here *H. diversicolor* colonizes areas of low salinity, and reproduces from March to April (ANSALONI *et al.*, 1986). However, the spawning period of this species varies between different geographic areas (SCAPS, 1992). The specimens may reach 20 cm in length in Italy, but their commercial size is from 10-12 cm. *H. diversicolor* is sold as "Tremolina", however, it is often confused with other species of the genus *Perinereis*. The cost in 1992 was about US $ 1 for a box of 8-10 worms. It is also imported from France.

***Perinereis cultrifera*** (Grube, 1840).

This species is common along the Italian coasts both in soft sediments and in shallow, algal covered hard bottoms. Commercial harvesting is mainly from the Venice Lagoon (ANSALONI *et al.*, 1986) (Fig. 1) where it thrives in shallow muddy bottoms forming burrows in the upper 10 cm. It is collected by shoveling and sieving the mud through large-mesh screens. Amateur anglers collect *P. cultrifera* from several other coastal areas, including the coasts of Sicily, where a $CuSO_4$ solution is used to force the worms out of their burrows. In the Venice Lagoon, *P. cultrifera* reproduces in March following epitokal modification (ANSALONI *et al.*, 1986).

Source : MNHN, Paris

However, other authors in the Mediterranean observed reproduction in different seasons and without epitoky (PÉRÈS & RANCUREL, 1948; DURCHON, 1957; MARCEL, 1962). In the Mediterranean *P. cultrifera* reaches a maximum length of 15 cm, while in the Atlantic it reaches 25 cm. The species is known commercially as "Saltarello veneziano", and it is often confused with *Perinereis rullieri* and sometimes with *H. diversicolor*. The commercial price is similar to that of *H. diversicolor* and a large number of *P. cultrifera* are also imported from France.

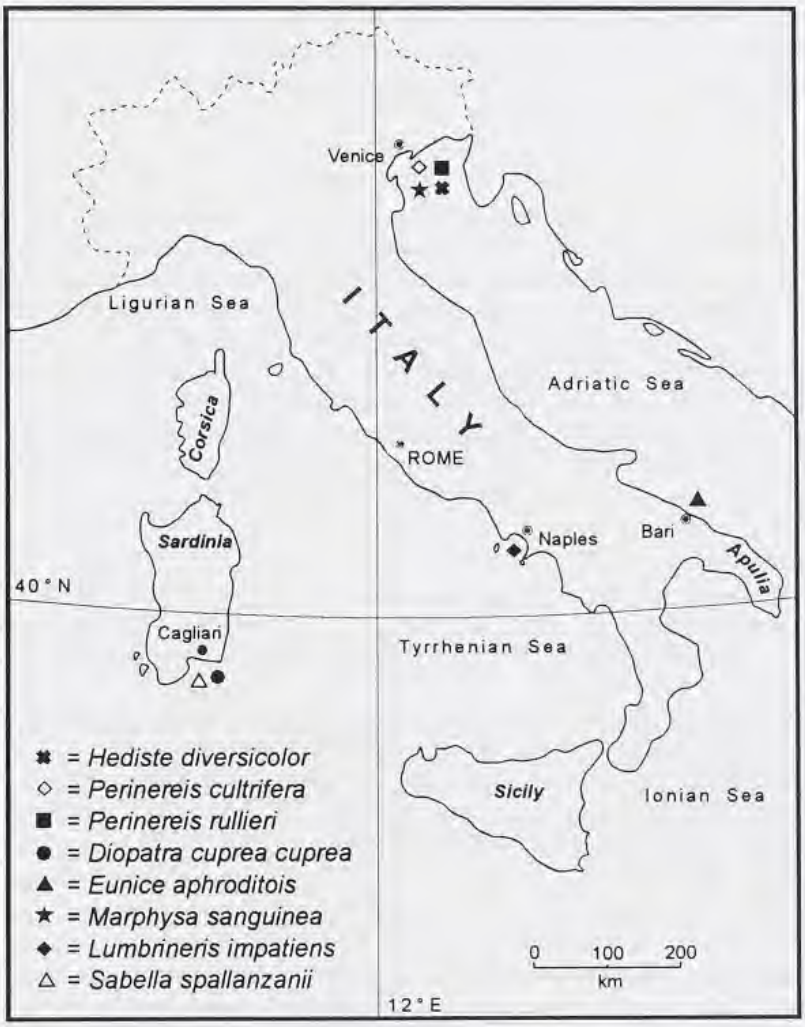



FIG. 1. — Map of Italy with the location of the main harvesting sites for each of the eigth species of polychaetes exploited as bait. Only the areas of intensive commercial collecting are indicated.

***Perinereis rullieri*** Pilato, 1974.

*P. rullieri* has been recorded only along the Italian coasts, and it is probably endemic to the Mediterranean Sea (PREVEDELLI *et al.*, 1990). The commercial digging occurs mainly in the Venice Lagoon where *P. rullieri* reaches 18-20 cm in length. It is harvested commercially from 8-10 cm. Worms are collected from the intertidal zone from a substrate of gravel, muddy sand and small stones (PREVEDELLI *et al.*, 1990). Spawning is generally in April, but not via epitoky, and fertilisation takes place on the bottom. Fertilized eggs are embedded in gelatinous envelopes which are attached to the stones where they form large, green coloured clumps. The hatched larvae are nectochaetae with three setigerous segments (PREVEDELLI *et al.*, 1990; PREVEDELLI & ZUNARELLI VANDINI, 1992). The species is often confused with the co-generic *P. cultrifera*, and is labelled and sold at the same prices of the other nereidids.

Source : MNHN, Paris

***Diopatra cuprea cuprea*** (Bosc, 1802).

Along the Italian coasts *D. cuprea cuprea* is found generally in shallow depths in sandy sediments mixed with mud. This species is commercially collected mainly in the littoral lagoon of Santa Gilla, near to Cagliari and in a few other shallow and sheltered areas nearby (Fig. 1) (COTTIGLIA, pers. comm). This species is sold as "Tremuligione", and is collected both using a spade in shallow water, and by SCUBA diving at 2 m depth. Number of bait diggers varies from about 25 in autumn and winter, to about 40 in spring and summer. The demand was great for this species, however, its harvest has been reduced recently because of the use of other local and imported bait worms (Cottiglia, pers. comm.). The number of worm dug depends on market demand and season, and ranges from a mean of 3-4,000 per day in winter, to a mean of 20, 000 in summer, resulting in an estimated 3.5 million of worms being harvested each year (Cottiglia, pers. comm.). *D. cuprea cuprea* can reach 30 cm in length but is collected from about 20 cm. Its reproductive cycle is unknown, but as other large onuphids (FAUCHALD, 1983), it could have a life span of several years.

***Marphysa sanguinea*** (Montagu, 1815).

*M. sanguinea* has been recorded from several Italian coastal areas in intertidal and shallow littoral muddy bottoms (PREVEDELLI, 1989). In the Venice Lagoon, where it is commercially harvested, it burrows deep in the sediment, below the layers colonized by the nereidids. The species grows to 50 cm in length, and specimens 20-30 cm long are used for commercial purposes. In the Venice Lagoon this species reaches a density up to 60 ind. $m^{-2}$, and it is collected by digging up sediment that is sieved through coarse screens. In the Venice Lagoon *M. sanguinea* reproduces seasonally in April, and without morphological modification. The spawning is synchronized and occurs on the bottom (PREVEDELLI, 1989). This species is the most valuable bait of all species collected in Italy. It is commonly sold as "Muriddo", with regional names of "Murone, "Bacone" and "Verme sanguigno". A box of 6-8 worms was sold in 1992 at about US $ 4. Specimens labelled as *M. sanguinea* are imported from the U.S.A. and Korea.

***Eunice aphroditois*** (Pallas, 1788).

*E. aphroditois* is a coastal species occurring at depths of 10-15 m in soft bottoms where it lives inside a characteristic U-shaped parchment tube. Small specimens may also occur on hard substrates (FAUVEL, 1923). In Italian waters it reaches over 1 m in length (BELLO, 1993), and specimens of larger dimensions have been reported from the Atlantic (FAUVEL, 1923). Reproduction and life cycle is unknown, however, because of the large size reached and like other related species (FAUCHALD, 1983; GIANGRANDE, 1989a), *E. aphroditois* may be a long-lived species. In Italy *E. aphroditois* is known as "verme di Rimini" and is mainly collected along the Apulia coasts (Fig. 1) where is called "Vermara". Worms are collected both by SCUBA diving up to 10 m depth, and by using a special long, thin stick from a boat (BELLO, 1993). *E. aphroditois* is a suitable bait to catch fish of the family Sparidae, and it is used also by commercial fishermen to bait their lines (BELLO, 1993). The price of a single specimen reached in 1992 US $ 1.5.

***Lumbrineris impatiens*** Claparède, 1868.

Along the Italian coasts *L. impatiens* is commonly reported in sandy, muddy-sand and detritic soft bottoms (GAMBI & GIANGRANDE, 1986) where it lives below the sediment in temporary burrows. Specimens collected in shallow waters (1-5 m depth) are of greater dimensions measuring up to 40 cm in length, than those collected from deeper waters (10-20 m) which are only a few centimeters in length. This suggests age class distribution according to depth, or an ecotype determined by different trophic and ecological conditions. However, the existence of "sibling" species cannot be excluded. The biology of *L. impatiens* is poorly known. MCNULTY & LOPEZ (1969) observed mature eggs throughout the year in Florida, but with a decrease in frequency in winter. CAZAUX (1972) studied the larval development of a population of the north Atlantic French coast, and he found that the larva is planctotrophic with a pelagic phase of about 15 days. Biological data of the Mediterranean Sea population of this species are lacking. For commercial purposes *L. impatiens* is mainly harvested from shallow sandy areas in the Gulf of Naples. Within the Gulf it is particularly abundant at the mouth of the Sarno river which is enriched with organic matter deriving from agricultural industry wastes. Worms are collected by about 10 SCUBA-divers who are organized in a cooperative. There is a great demand for this species which is locally called "Esca rossa" or also "Tremolina". A single diver may collect over 200 worms a day. The commercial size of the worms is generally over 20 cm long and the cost in 1992 varies form US $ 0.5 to US 1 $ for a single specimen.

Source : MNHN, Paris

***Sabella spallanzanii*** (Gmelin, 1791).

*S. spallanzanii*, better known under its original generic name of *Spirographis*, is very common on hard substrate along the Italian coasts (GIANGRANDE, 1989, b). It is found in the open coastal areas from 1 to 30 m depth, and in shallow confined areas such as harbours, where it often reaches very high densities. *S. spallanzanii* reproduces in winter, and the egg dimensions suggest a lecithotrophic development (GIANGRANDE & PETRAROLI, in press). Specimens can reach up to 40 cm in length and preliminary observations suggest a growth rate of about 10 cm per year (GIANGRANDE & PETRAROLI,1994). Since this species is a suspension feeder, it can be fed in laboratory with various kinds of suspended food, including probably particulate organic matter, and it may be suitable in the treatment of domestic and aquaculture wastes. The use of this species as a bait by anglers is limited to some localities in Sardinia where it is known as "Tremuligione amaro". It seems particularly suitable as bait for catching large Sparidae (RIGHINI, 1991). The potential for a larger market for this species is supported by the results of some preliminary tests conducted with amateur anglers (GIANGRANDE, unpublished data). It is also likely that other large-sized sabellids with growth rate and ecological requirements similar to those of *S. spallanzanii* may be suitable for bait (*e.g.*, *Branchiomma luctuosum* (Grube)) (SORDINO & GAMBI, 1992).

A few other polychaete species belonging to the genera *Sabellaria* and *Ophelia*, are collected as bait in various coastal areas by local amateur anglers, but are not commercialized. A list of some of the polychaete species harvested as bait in Italy and in other countries is given in Table 1. The list is probably incomplete and the number of species taken is likely underestimated because such information is usually not reported. However, about 32 species are exploited in various countries, and share some general features : a) relatively large adult dimensions (between 15 to 30 cm in length); b) wide geographic and ecological distribution, indicating a broad tolerance to different environmental conditions; c) a variety of feeding behaviour and food sources, with most of them being detritivores or omnivores; d) life spans generally longer that one year, and frequently 3 to 5 years; e) many are polytelic (= iteroparous) species breeding more than once per lifetime, but some (*e.g.*, Nereididae and Glyceridae) are monotelic (= semelparous) (OLIVE, 1983). The life span of the monotelic species varies between 1-2 years in the case of *H. diversicolor*, and up to three or more years in others.

## OTHER APPLICATIONS AND USES OF POLYCHAETES

Small-sized polychaetes, such as various Spionidae and Capitellidae, are used in aquaculture to supplement the diet of commercial fish and crustaceans (GUÉRIN, 1978). These species generally show many "r-strategy" traits in their life histories. In an integrated polyculture system for the treatment of acquaculture wastes, *Capitella capitata* was used as food for juvenile stages of the commercial fish *Pseudopleuronectes americanus* (RYTHER *et al.*, 1975). In a semi-intensive culture of *Penaeus japonicus* in Italy, the spionid polychaete *Polydora ciliata* played an important role in the diet of the shrimp and was consumed in large amounts from the bottom of the culture tanks (ZUPO *et al.*, 1989). Several species of spionids and capitellids are relatively easy to rear in the laboratory from larvae collected from plankton, (CHU & LEVIN, 1989). The culture of spionids throughout their life cycle has been documented for *Malacoceros fuliginosus* (GUÉRIN, 1987), for *Boccardia semibranchiata* (GUÉRIN, 1991) and for *Streblospio benedictii* (LEVIN, 1984). *Spio decoratus* has been reared from larvae collected in plankton to mature adults (GIANGRANDE *et al.*, 1992). This species is polytelic, a feature common to several Spionidae (GUDMANSSON, 1985). It has a short life span and reproduces continuously after reaching maturiry at six months ; egg laying then occurs about every other month. The above studies suggest that several species of spionids may be suitable to be reared in the tanks with cultured fish and crustacean to supplement their diet.

## DISCUSSION

The bait polychaetes which are commercially the most valuable in Italy are likely to be the species with the longest life spans: *M. sanguinea*, *L. impatiens*, *D. cuprea cuprea* and *E. aphroditois*. Because of their long life cycle, the long term exploitation of these species needs a knowledge of their biological and ecological requirements for management that optimizes their harvest and minimises the impact of collecting on their populations and on their habitat. However, apart from *M. sanguinea* and *P. rullieri*, studies on the life cycle and population dynamics

Source : MNHN, Paris

TABLE 1. — Bait species harvested and/or cultured in Italy and in other countries. The data are from literature, market surveys and other sources.

| |
|---|
| *Neanthes virens* Sars is harvested in the U.S.A. (sandworm, CREASER *et al.*, 1983), in Spain (SARDÀ, 1989) and U.K. (BLAKE, 1979a) where it is also industrially cultured (OLIVE, 1994) and exported to Italy and other countries. |
| *Neanthes arenaceodentata* (Moore) is cultured and sold as test animal for aquatic and sediment toxicological testing (REISH, 1980). |
| *Neanthes* spp., two species (*N. succinea* (Leuckart) and *N. caudata* Delle Chiaje) are collected in France (BELLAN, pers. comm. ) and Spain (SARDÀ, 1989). |
| *Neanthes japonica* (Izuka) is harvested and cultured in Japan (KURIHARA, 1983). |
| *Perinereis nuntia vallata* (Grube) is harvested and cultured in Japan (KURIHARA, 1983) and imported to Italy (named "cinese" ). |
| *Perinereis vancaurica* (Ehlers) is harvested in Korea and imported to Italy, where it is sold as "coreano". |
| *Perinereis aibuhitensis* Grube is collected in south-east Asia; it is imported to Italy and sold as "coreano" or "cinese". |
| *Perinereis brevicirris* (Grube) is cultured in Taiwan (CHEN, 1990; OLIVE, 1994). |
| *Perinereis cultrifera* (Grube) is harvested in Italy (Ansaloni *et al.*, 1986) and in France (BELLAN, 1964). |
| *Perinereis rullieri* Pilato is collected in Italy (Venice Lagoon) (present paper). |
| *Hediste diversicolor* (O.F. Müller) is harvestd in Italy (ANSALONI *et al.*, 1986) and in France (BELLAN, 1964). |
| *Pseudonereis variegata* Ehlers is collected from South Africa (VAN HERWERDEN, 1989). |
| *Nephtys caecoides* Hartman is collected in Northern California and Oregon where it is used in marine toxicological testing (REISH, pers. comm.). |
| *Nephtys* spp., two species (*N. hombergii* Audouin & Milne Edwards, and *N. cirrhosa* Ehlers) are collected in Spain (Sardà, 1989) and U.K. (OLIVE, pers. comm.). |
| *Glycera dibranchiata* Ehlers is harvested in the USA ("bloodworm", CREASER *et al.*, 1983) and it is exported to Italy where it is sold as "americano" or "canadese". |
| *Halla parthenopeia* (Delle Chiaje) is collected and greatly valued in Spain (SARDÀ, 1989) . |
| *Lumbrineris latreilli* Audouin & Milne Edwards is collected in Spain (SARDÀ, 1989) . |
| *Lumbrineris impatiens* Claparède is collected in Italy (GAMBI *et al.*, 1992, present paper) and in Spain (Sardà, 1989). |
| *Hyalinoecia tubicola* (O.F. Müller) was collected in Spain (SARDÀ, 1989). |
| *Diopatra cuprea cuprea* (Bosc) is harvested in Italy (Sardinia, GAMBI *et al.*, 1992, present paper). |
| *Onuphis teres* Ehlers is collected in Australia (OLIVE, 1994). |
| *Eunice aphroditois* (Pallas) is collected in Italy (BELLO, 1993; present paper). |
| *Marphysa sanguinea* (Montagu) is collected in Italy (ANSALONI *et al.*,1986), in Spain (SARDÀ, 1989), in France (BELLAN, 1964), in U.S.A. and Korea (CHOI, 1985) and in Australia (OLIVE, 1994). |
| *Arenicola marina* L. is collected in The Netherlands (Heilingeberg, 1982), along the Atlantic coasts of Spain (SARDÀ, 1989), U.K. and Ireland (OLIVE, 1994), and U.S.A. (D'ASARO & CHEN, 1976). |
| *Arenicola cristata* Stimpson is collected along the northern Mediterranean coasts of Spain (Catalonia; SARDÀ, 1989) and in the U.S.A. (D'ASARO , 1973). |
| *Arenicola brasiliensis* Nonato. This species is reported among the various lugworms collected as bait (D'ASARO , 1973). |
| *Capitellidae* gen. spp. Various species (probably of the genus *Notomastus)* are collected in Spain (SARDÀ, 1989). |
| *Ophelia* spp. Various species are collected occasionally by amateur anglers both in Italy and in Corsica (BELLAN, pers. comm.). |
| *Sabellaria* spp. Various species are occasionally collected in a few localities along the Italian coasts (GAMBI *et al.*, 1992). |
| *Sabella spallanzanii* (Gmelin) is collected in a few localities in Sardinia (Italy) (present paper). |

of the commercial species in the exploited sites in Italy are lacking. They are harvested with no regard to their life history and the potential destructive effects of collecting. Moreover, worms are generally harvested without appropriate legislation to regulate periods of collecting and number of individuals which can be removed.

Geographic variability in reproductive mode and time has been documented in different cospecific populations (*e.g., H. diversicolor* or *P. cultrifera*). In addition, population structure may vary and not all populations may be commercially viable (OLIVE, 1994). A few studies have examined how harvesting may affect population parameters such as fecundity, growth rate, mortality and genetic variability. The spawning stock and the population structure of *Glycera dibranchiata* (KLAWE & DICKIE, 1957) and of *Neanthes virens* and *Arenicola marina* (BLAKE, 1979 a, b) were not effected by digging. On the other hand, for a different population of *Glycera*

Source : MNHN, Paris

*dibranchiata*, intensive harvesting reduced heterozygosity, enhanced genetic drift and altered rapidly the genetic structure of the population (VADAS & BRISTOW, 1985).

The commercial harvesting of polychaetes also has general implications at community and environmental level, and raises problems of resource management that are common to other cases of marine resource exploitation. Digging for worm collection causes great physical disturbance to the substrate and this affects the benthic community. A study on the rocky coasts of South Africa (VAN HERWERDEN, 1989) demonstrated dramatic destruction of the environment and of biotic resources, particularly mussel beds, caused by the collection of *Pseudonereis variegata*. Digging for the bait *Arenicola marina* along the Norfolk coast (U.K.) caused massive death of the cockle, *Cerastoderma edule* (JACKSON & JAMES, 1979). On the other hand, investigations on the effects of digging for *Arenicola* on a tidal flat in The Netherlands (HEILIGENBERG, 1982) and on an estuary in the U.K. (MCLUSKY *et al.*, 1983) revealed that, after an initial period of community collapse, the density of some benthic species was enhanced, and there was a rapid population recovery of the worms, mainly due to the above-surface migration of adults from surrounding areas. A similar recolonization pattern, observed for a different population of *Arenicola* (OLIVE, in press), suggests that periods of exploitation alternating with periods of recovery from reserve zones could be a suitable management method for this species, as well as for other exploited worms (*e.g.*, *M. sanguinea*; CHOI, 1985).

These few reports and their different results demonstrate the need for systematic studies to evaluate the environmental impact of long term exploitation of worm populations. There is an increasing awareness of this problem also in the Venice Lagoon and in other Italian areas where habitat damage coupled with competition among professional and amateur fishermen is starting to limit these worm resources (BELLO, 1993).

Another important environmental risk is that the importation of allochtonous species which are generally sold alive (in Italy mainly the tropical *Perinereis* spp.), may increase the risk of accidental introduction of foreign taxa. To reduce and overcome these environmental problems, commercial rearing is an attractive solution both scientifically and economically. To date a few polychaete species are commercially reared (RYTHER *et al.*, 1975 ; REISH, 1980; KURIHARA, 1983; OLIVE, 1994), and various biological problems related to their large scale production, such as diseases, parasites, supply of larvae, still need to be resolved (SCAPS, 1992; OLIVE, in press, a). Some of the Italian species are potentially suitable for commercial culturing. Those species are the nereidids that have short life spans, and *M. sanguinea* or *L. impatiens* that can fed various organic detritus. *S. spallanzanii* which has a fast growth rate and can utilize organic compounds produced and released in the water column by other cultured organisms (*e.g.*, mussels) is another potential species.

The main aim and the scientific challenge of the research on the biology of the bait polychaete species should be to develop rearing techniques for intensive production that, increasing resource supply, would greatly reduce the harvest impact on natural populations, associated organisms and biotopes.

## ACKNOWLEDGEMENTS

We wish to thank Dr. P.J.W. OLIVE and Prof. D. REISH for their critical reading of the manuscript and the usefull comments. Thanks are also due to Dr. R. SARDÀ BORROY for data on collection of worm bait species along the Spanish coasts, and to Dr. C. COTTIGLIA for harvesting data on *Diopatra cuprea cuprea* in the Santa Gilla lagoon (Sardinia, Italy).

## REFERENCES

ANSALONI, I., PELLIZZATO, M., PREVEDELLI, D., ZUNARELLI VANDINI, R., 1986. — Policheti di interesse economico nella laguna di Venezia *Nova Thalassia*, **8**, suppl. 3 : 641-642.

BELLAN, G., 1964. — Contribution à l'étude systématique, bionomique et écologique des annélides polychètes de la Méditerranée. *Rec. Trav. St. mar. Endoume*, **49** (33) : 1-371.

BELLO, G.B., 1993. — La pesca della vermara in provincia di Bari. *Umanesimo della pietra verde* (Bari, Italy), **8** : 1-12.

BLAKE, R.W., 1979a. — On the exploitation of a natural population of *Nereis virens* Sars from the North-east coast of England. *Estuar. Coast. Shelf Sci.*, **8** : 141-148.

BLAKE, R.W., 1979b. — Exploitation of a natural population of *Arenicola marina* (L.) from the North-east coast of England. *J. appl. Ecol.*, **16** : 563-670.

Source : MNHN, Paris

CAZAUX, C., 1972. — Développement larvaire d'annélides polychètes (Bassin d'Arcachon). *Arch. Zool. exp. gén.*, **113** : 71-108.

CHEN, L.C., 1990. — *Aquaculture in Taiwan*. Fishing News Books, Oxford : 273pp.

CHOI, I.H., 1985. — Lugworms: from harvesting to exporting. *Infofish Marketing digest*, **6** : 49-52.

CHU, J.W., & LEVIN, L., 1989. — Photoperiod and temperature regulation of growth and reproduction in *Streblospio benedictii* (Polychaeta, Spionidae). *Inv. Repr. Develop.*, **15** : 131-142.

CREASER, E.P., CLIFFORD, D.A. Jr, HOGAN, M.J., SAMPSON, D.B., 1983. — A commercial sampling program for sandworms, *Nereis virens* Sars, and bloodworms, *Glycera dibranchiata* Ehlers, harvested along the Maine coast. *NOAA technical report NMFS SSRF-767* : 1-56.

D'ASARO, C.N., 1973. — Cultured lugworms- a new source of bait for marine sport fishermen. *Am. Fish. Farmer*, **4** : 4-7.

D'ASARO, C.N. & CHEN, C.K., 1976. — Lugworm aquaculture. Florida Seagrant Program, report n° **16**, 114 pp.

DURCHON, M., 1957. — Problèmes posés par le comportement des néréidiens au moment de leur reproduction. *Ann. Biol.*, **33** : 31-42.

FAUCHALD, K., 1983. — Life diagram patterns in benthic Polychaetes. *Proc. biol. Soc. Wash.*, **96** : 160-177.

FAUVEL, P., 1923. — Polychètes errantes. *Faune Fr.*, **5** : 1-488.

GAMBI ,M.C., & GIANGRANDE, A., 1986. — Distribution of soft-bottom Polychaetes in two coastal areas of the Tyrrhenian sea (Italy) : structural analysis. *Estuar. coast. Shelf Sci.*, **23** : 847-862.

GAMBI, M.C., LANERA, P., SORDINO, P., 1992. — Conoscenze attuali sulla raccolta e l'allevamento di Anellidi Policheti a fini economici. *Oebalia*, **17**, Suppl. : 219-221.

GIANGRANDE, A., GRAVINA M.F., GAMBI, M.C., FRESI, E., ARDIZZONE, G., 1983-84. — Policheti di fondo mobile di aree costiere semichiuse : fattori di selezione in ambiente salmastro. *Nova Thalassia*, **6** suppl. : 155-163.

GIANGRANDE, A., 1989a. — Observations on recruitment and growth of *Eunice harassii* Audouin & Milne Edwards (Polychaeta, Eunicidae) in the Mediterranean sea. *Vie Milieu*, **39** : 135-141.

GIANGRANDE, A., 1989b. — Censimento dei Policheti dei mari italiani: Sabellidae Malmgren, 1867. *Atti Soc. Tosc. Sc. Nat. Mem., Serie B*, **96** : 153189.

GIANGRANDE, A., QUARTA S., CAROPPO, C., 1992. — Observations on *Spio decoratus* (Polychaeta, Spionidae) life-history under laboratory conditions, with taxonomic notes. *Oebalia*, **18** N.S. : 83-93.

GIANGRANDE, A., & PETRAROLI, A., 1994. — Preliminary observation on reproductive cycle and growth of *Sabella spallanzanii* (Gmelin) (Polychaeta, Sabellidae) in the Mediterranean sea. *Mem. Mus. natn. Hist. nat.*, **162** : 51-56.

GUDMANSSON, G., 1985. — Life history patterns of polychaete species of the family Spionidae. *J. mar. biol. Ass. U.K.*, **65** : 93-111.

GUÉRIN, J.P., 1978. — Intérêt de l'élevage des Polychètes du point de vue de la mariculture. *Oceanis*, **4** : 13-22.

GUÉRIN, J.P., 1987. — Élevage de Spionidés (Annélides, Polychètes) en cycle complet. 1. Techniques d'élevage de l'une des trois formes de *Malacoceros fuliginosus* des côtes françaises. *Aquaculture*, **62** : 215-257.

GUÉRIN, J.P., 1991. — Élevage de Spionidés (Annélides, Polychètes) en cycle complet : 3. Description du développement larvaire de *Boccardia semibranchiata*. *Annles Inst. Océanogr., Paris*, **67** : 145-154.

HERWERDEN VAN, L., 1989. — Collection of mussel worms *Pseudonereis variegata* for bait- a legislative anachronism. *S. Afr. J. mar. Sc.*, **8** : 363-366.

HEILIGENBERG VAN DEN, T., 1982. — The effects of mechanical digging for lugworms *(Arenicola marina L.)* on the benthic fauna of the tidal flats in the Dutch Wadden Sea. *Hydrobiol. Bull.*, **16** : 291-292.

JACKSON M.J., & JAMES R., 1979. — The influence of bait digging on cockle, *Cerastoderma edule*, populations in Norfolk. *J. appl. Ecol.*, **16** : 671-679.

KLAWE, W.L. & DICKIE, L.M., 1957. — Biology of the bloodworm, *Glycera dibranchiata* Ehlers, and its relation to the bloodworm fishery of the Maritime Provinces. *Fish. Res. Brd Canada. Bull.*, **115** : 1-37.

KURIHARA, Y., 1983. — Study of domestic sewage waste treatment by the Polychaetes *Neanthes japonica* and *Perinereis nuntia* var. *vallata*, on an artificial tidal flat. *Int. Revue ges. Hydrobiol.*, **68** : 649-670.

Source : MNHN, Paris

LEVIN, L., 1984. — Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of north America. *Biol. Bull.*, **166** : 494-508.

MARCEL, R., 1962. — Cycle annuel de *Perinereis cultrifera* Grube (Annélide Polychète) à Alger. *Mem. Soc. Sci. Nat. Math. Cherbourg*, **49** : 39-54.

McLUSKY, D.S., ANDERSON, F.E., WOLFE-MURPHY, S., 1983. — Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait digging. *Mar. Ecol. Progress Series*, **11** : 173- 179.

McNULTY, J.K. & LOPEZ, N.N., 1969. — Year-round production of ripe-gametes by benthic Polychaetes in Biscayne Bay, Florida. *Bull. mar. Sc.*, **19** : 945954.

OLIVE, P.J.W., 1983. — Annelida Polychaeta. In: Adiyoti K.G. and Adiyodi R.G.(eds.), *Reproductive biology of invertebrates, vol. I : oogenesis, oviposition and oosorption* : 357-422.

OLIVE, P.J.W., 1994. — Polychaeta as a world resource: patterns of exploitation, management and the potential for aquaculture based production. *Mem. Mus. natn. Hist. nat.*, **162** : 603-610.

OLIVE, P.J.W., in press. — Management of the lugworm *Arenicola marina* and the ragworm *Nereis virens* (Polychaeta) in conservation areas : the importance of population structure and recruitment processes. *Aquatic Conservation.*

PÉRÈS, J.M., & RANCUREL, P., 1948. — Observations sur la ponte de *Perinereis cultrifera* Grube dans le golfe de Marseille. *Bull. Soc. zool. France*, **73** : 97-100.

PREVEDELLI, D., 1989. — *Studio di una popolazione di Marphysa sanguinea (Montagu) (Polychaeta, Eunicidae) nella laguna di Venezia: approccio autoecologico*. Doctoral Thesis, University of Modena (Italy), 267pp.

PREVEDELLI, D., CASTELLI, A., ABBIATI, M., ZUNARELLI VANDINI, R., 1990. — Distribution and life cycle of *Perinereis rullieri* Pilato (Polychaeta, Nereididae), a mediterranean endemism. *Rapp. P.-v. Comm. int. Mer Medit.*, **32** : 19.

PREVEDELLI, D., & ZUNARELLI VANDINI R., 1992. — Ciclo biologico di *Perinereis rullieri* Pilato (Polychaeta : Nereididae) nella laguna di Venezia. *Oebalia*, **17**, Suppl. : 309-313.

REISH D., 1980. — *The effects of different pollutants on ecologically important polychaete worms*. U.S. Environmental Protection Agency, Narragansett, Rhode Island, EPA-600/3-80-053, 138pp.

RIGHINI, A., 1991. — Spirografo (*Spirographis spallanzanii*). *Pesca in Mare*, September, 1991, **9** : 28-29.

RYTHER, J.H., GOLDMAN, J.C., GIFFORD, C.E., HUGUENIN, J.E., WING, A.S., CLARNER, P.J., WILLIAMS, L.D. & LAPOINTE, B.E., 1975. — Physical integrated waste-recyclingg-marine polyculture systems. *Aquaculture*, **5** : 163-177.

SARDA BORROY, R., 1989. — *Informe Tecnico*. Escuela Spencer de Administracion y Direccion de Empresas (ESADE): 190 pp.

SCAPS, P., 1992. — *Bases biologiques de l'élevage de deux espèces d'Annélide Polychaetes :* Nereis diversicolor *(O.F. Muller) et* Perinereis cultrifera *(Grube)*. Doctorat Univ. Rennes I (France) : 171 pp.

SORDINO, P., & GAMBI, M.C., 1992. — Prime osservazioni sulla biologia riproduttiva e sul ciclo vitale di *Branchiomma luctuosum* (Grube, 1869) (Polychaeta, Sabellidae). *Oebalia*, **17** (2) Suppl. : 425-427.

TENORE, K.R., & GOPALAN, U.K., 1974. — Feeding efficiencies of the Polychaete *Nereis virens* cultured on hard-clam tissue and oyster detritus. *J. Fish. Res. Brd Canada*, **31** : 1675-1678.

TENORE, K.R., BROWNE M.G., CHESNEY, E., 1974. — Polyspecies aquaculture systems : the detrital trophic level. Sears Foundation. *J. mar. Res.*, **32** : 425-432.

VADAS, R.L., & BRISTOW, G., 1985. - Genetic changes associated with a bottleneck in an overharvested population of *Glycera dibranchiata* (Polychaeta). *In:* J.S. GRAY & M.E. CHRISTIANSEN, Jr. (eds.), *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*. Wiley & Sons Ldt. : 617-629.

ZUPO, V., LUMARE, F., BISIGNANO V., PAVONE 1989. - Ruolo delle associazioni bentoniche nell'allevamento di *Peneaus japonicus* Bate : Relazioni ponderali. *Nova Thalassia*, **10**, suppl. 1 : 297-308.

Source : MNHN, Paris

Source : MNHN, Paris

# Polychaeta as a world resource: a review of patterns of exploitation as sea angling baits and the potential for aquaculture based production

*Peter J. W. OLIVE*

Department of Marine Sciences and Coastal Management
University of Newcastle upon Tyne
Newcastle upon Tyne, NE1 7RU, United Kingdom

ABSTRACT

Exploited Polychaeta are drawn from several families notably: Arenicolidae, Glyceridae, Nereidae, Nephtyidae and Eunicidae. Worms have been exploited as bait for sport and commercial fishing operations for generations but new demands for polychaete biomass arise from the growth of the aquaculture industries for finfish and Crustacea. Several types of exploitation can be recognised ranging from the collection of worms by sport fishermen from local populations primarily for their "own use", to highly organised collection on a commercial scale with nationally important economic value. There is increasing concern about the environmental impact of both professional and amateur bait digging. Two case studies where exploitation was in conflict with conservation proposals are discussed. They show that the management of stocks for sustainable yield may be incompatible with conservation interests but some populations may be amenable to effective management. Substantial fisheries for bait have developed in Korea, China, NE USA and, on a smaller scale, in Europe to meet the demand for bait by sport fishermen. In Europe demand exceeds supply and both importation and intensive aquaculture have developed to supplement the supplies taken from the natural environment in european coastal regions; the management implications of these developments are discussed.

RÉSUMÉ

**Les Polychètes en tant que ressources mondiales : revue des systèmes d'exploitation comme appâts et potentiel pour une production par aquaculture**

La majorité des polychètes d'intérêt économique sont des membres des familles des Arenicolidae, Glyceridae et Nereidae ; quelques espèces appartiennent à l'ordre Eunicida. Depuis des siècles les vers marins sont utilisés comme appâts par les pêcheurs professionnels et amateurs. De nos jours la demande s'intensifie en raison de l'essor de la pêche de loisir et du développement de l'aquaculture des crustacés et des poissons. L'exploitation des vers consiste dans leur récolte par les pêcheurs sportifs pour leur usage personnel et dans celle, bien organisée, effectuée par les professionnels à des fins commerciales ; la valeur économique de cette dernière, liée à l'exportation sur les marchés mondiaux, est loin d'être négligeable au plan national. Ainsi sur les 1500 à 2000 tonnes de polychètes qu'utilise le Japon, la plus grande part est importée. Mais la collecte des vers n'est pas sans effet sur le milieu naturel ; à cet égard, les résultats de deux études traitant des conflits d'intérêt entre exploitation et protection de l'environnement sont présentés à titre d'exemple. Des centres de

OLIVE, P.J.W., 1994. — Polychaeta as a world resource: a review of pattern of exploitation as sea angling baits and the potential for aquaculture based production. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 603-610. Paris ISBN 2-85653-214-4

Source : MNHN, Paris

production importants, destinés à satisfaire les besoins des pêcheurs sportifs, ont été créés particulièrement en Corée, en Chine, aux Etats-Unis et à une moindre échelle en Europe où la demande dépasse largement la production naturelle. Par conséquent l'accroissement des importations et le développement conjoint de l'aquaculture s'avèrent indispensables pour alimenter le marché européen.

## INTRODUCTION

The Polychaeta play an important role in the ecology of marine communities partly due to the diversity of their structure and function. A relatively small number of species are also of commercial importance. This arises mostly from their use as live bait in support of the sea angling industry which in some developed economies is the single largest participatory leisure activity. The Polychaeta are likely to become increasingly important as a resource in relation to the development of world aquaculture for Crustacea (Penaeidae) since it has been found that polychaetes can provide a nutritionally correct balance of polyunsaturated fatty acids which are essential for egg maturation in cultured prawns (LYTLE *et al.*, 1990) or can provide other factors essential for egg maturation (CROZ *et al.*, 1988).

The markets for Polychaeta have characteristics which give suitable live polychaete biomass particularly high monetary value, considerably higher for instance than is obtained in most markets for human food.The value of polychaetes varies of course between markets and like any commodity is also subject to short term fluctuations. The price of ragworms from the USA fishery in Maine rose sharply from mid 1950's and then remained relatively high. The value in dollars per thousand worms to the Maine fishery increased from about $15 per thousand in 1960 to c.$38 per thousand in 1980. CREASER *et al.* (1983) and CREASER & CLIFFORD (1986) give values for the Maine (USA) bait worm fishery and CHOI (1985) discusses the value of Korean bait worm export markets. In general whole sale values of $US 0.1 per specimen or 15-25 US$ per Kg have been sustained over a number of years in the USA and Japanese markets while values in the European markets appear to be even higher, current wholesale values being in the region of $70 - $90 per thousand worms according to size. There is also evidence of substantial added value in distribution and marketing.

In the scientific literature bait digging has been discussed primarily in relation to the potential impact on marine communities. CREASER & CLIFFORD (1982, 1986) and CREASER *et al.* (1983) however discuss the characteristics of the Maine (USA) fishery and the population dynamics of the two bait species (*Nereis virens* and *Glycera dibranchiata*) that are exploited commercially in that fishery. Details of the life history of *G. dibranchiata* in relation to the fishery were also provided by KLAWE & DICKIE (1957) and SIMPSON (1962).

There is no doubt that bait digging is the cause of serious environmental disturbance (CRYER *et al.*, 1987; JACKSON & JAMES, 1979; MCLUSKY *et al.*, 1983; VAN DEN HEILIGENBERG, 1987) but it would be wrong to draw simplistic conclusions. There is a wide variety of bait digging activity ranging from the collection of bait by individual anglers for their own use to fully organised professional activity. Each will have its own particular effects on biological communities (see OLIVE, 1993 for discussion of two case histories).

The bait supply industry has a crucial role in the support of sea angling - a world wide leisure industry including manufacturing and distribution of hard ware and many associated tourism and leisure time related commercial activities - and in some economies it represents a very significant contribution to the local economy (see CHOI 1985; CREASER *et al.*, 1983 for discussion).

The high price of the worms supplied to the sea angling leisure industry reflects the relative shortage and labour intensive nature of current supply routes. This paper will review the patterns of supply and consider the management options and the potential for the application of aquaculture techniques to polychaete production which would ameliorate the potential conflict between the market and the demands of environmental conservation.

## PRINCIPLE POLYCHAETE BAIT SPECIES AND PATTERNS OF EXPLOITATION

The principle species of Polychaeta used as bait are listed in Table 1 together with the principle countries of origin and known export destinations.

The most important species are the European lugworm (*Arenicola marina* L.), the North American sand worm / European ragworm (*Nereis virens* Sars), the Korean blue ragworm (*Perinereis* spp.), Korean red ragworm (*Marphysa sanguinea*) and the American blood worm (*Glycera dibranchiata* Ehlers). All of these species support well established commercial fisheries that have been sustained over several decades. Such fisheries can only develop

Source : MNHN, Paris

on substantial populations and the fishery frequently has an important role in the host economy. Management of the fishery as a sustainable natural resource is then an important objective. The location of these major fisheries for Polychaeta and the distribution routes from them are shown in figure 1.The main routes of distribution are i) from the South China Sea (Korea and mainland China) into Japan but with an increasing quantities being transported from Korea to Europe and USA; ii) from NE Coast of USA (Maine) to Gulf States and California in USA, and to Europe. Within Europe there is substantial distribution of ragworms from Northern coastal regions (Netherlands, N. Ireland, Brittany) to the Mediterranean coasts and distribution from Venetian lagoon to southern Italy. Since the worms are distributed live and used in the natural habitat there is a potential impact on the geographical distribution of some species.

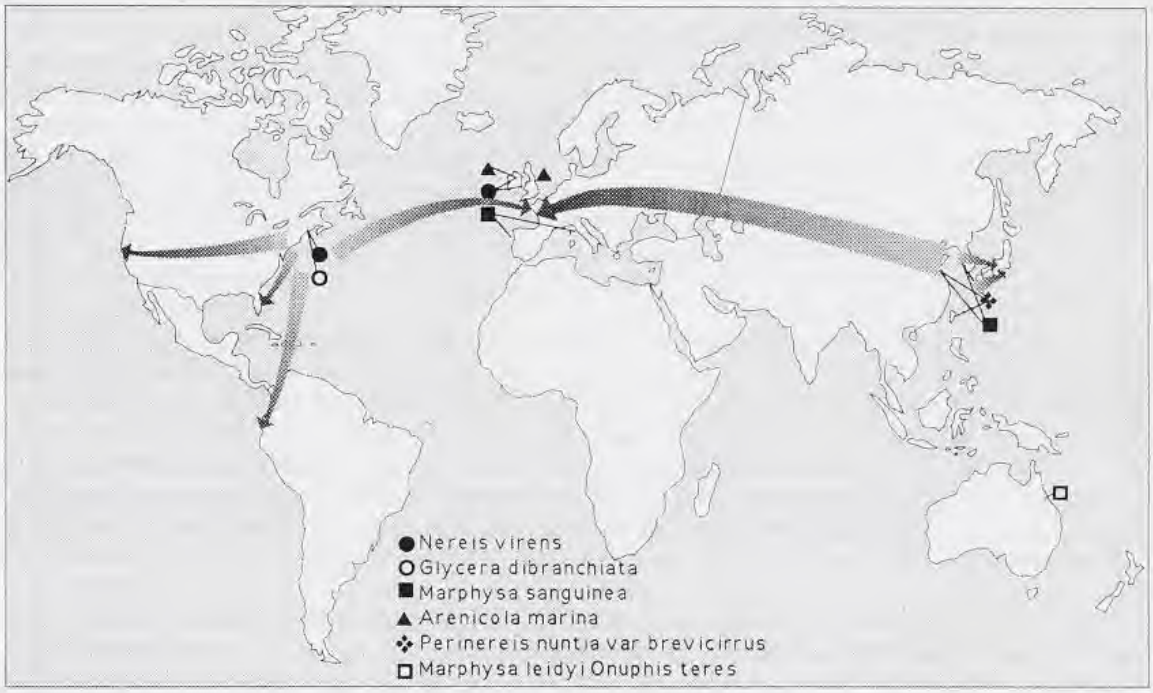



FIG. 1. — Map showing some of the principle centres for the commercial exploitation of bait worms and the pattern of distribution from them.

CHOI (1985) gives values for the export of the two Korean bait worms. The peak export volume recorded was in 1979 when some 900 metric tonnes were exported, most was sent to Japan, but 27.4 tonnes were exported to France. The export of substantial quantities of material from this source to Europe has continued and exports to Japan may have increased in recent years.

CREASER *et al.* (1983) discuss the economics of the Maine fishery and attempt to evaluate the catch per unit effort. The analysis of the data suggests that the Maine bait fishery is restricted by limited entry and that the optimal sustainable yield (OSY) can be related to the numbers of diggers for each species in the fishery. The authors suggest that peak catch is at about 36 million worms (*N. virens* and *G. dibranchiata* combined) per annum representing the effort of "very roughly" 1,100 licensed diggers and representing the supply of c.180 tonnes to the world markets.

A similar analysis of major European and Far Eastern fisheries for bait worms is urgently required.

In addition to these fisheries there is, in many countries, a long established tradition of collection of bait by anglers for their own use and there is a gradual transition from this type of exploitation through ad hoc / opportunistic commercial exploitation to fully professional digging for bait with organised distribution. OLIVE (1993) investigated the impact of bait collection on local populations of bait species in conservation areas and suggested a classification of bait collection that would take into account the marked differences between substantial sustainable fisheries and other forms of collection (see below).

Source : MNHN, Paris

Three types of exploitation can be recognised :

- Type I. — Collection by anglers for their own use.
- Type II. — Collection by semi-professional bait diggers for ad hoc commercial sales.
- Type III. — Collection by professional diggers contracted to wholesaler/distributors.

Each type of bait collection will develop under different circumstances and will generate different management problems but in general bait digging of Types I (own use) and Type II (ad hoc semi-professional digging) are more likely to be directed at non-sustainable resources than Type III as discussed above. Conflicts between Types I and II are to be expected. A particularly worrying development is the appearance of teams of itinerant professional diggers targeting non-sustainable resources as is now happening in the South of England and elsewhere in Europe.

Type I exploitation — Anglers digging bait for their own use will only give rise to resource management problems near substantial centres of population or in areas where there is inward movement of leisure anglers from urban centres but in such areas the problems may become acute. In the UK a variety of measures have been taken by local authorities and conservation agencies to restrict access for bait digging purposes in some beaches (OLIVE , 1993). This may involve the designation of specific areas for bait digging. To be effective an accurate estimate of both demand and sustainable yield is required but this information is not usually available to the legislators.

The most severe management problems are associated with the temporary use of resources by semi-professional bait diggers for whom bait digging is not the main or sole source of income. In these circumstances the over-exploitation of resources may be severe. Since the exploitation is opportunistic there is likely to be chronic over-exploitation of dwindling stocks. When the return per unit effort falls below a profitable level the bait digging pressure will be reduced and diggers will look elsewhere so that beaches will be subject to alternating periods of depletion and subsequent recovery.

OLIVE (1993) described such a situation in NE England in which a designated area of an estuary (Budle Bay) containing substantial population of the lugworm *A. marina* was set aside for bait collection. The project was discussed in detail with a local Sea Angling Association and was designed to provide local anglers with access to bait within a National Nature Reserve within which for conservation purposes bait collection would more generally be restricted. The area set aside was substantial - approx 200 m x 2 km but it was totally deprived of lugworms within six weeks of the onset of bait digging. It was estimated that in this case some 4 million worms were taken in this time. The management plan had seriously underestimated the predation pressure on the beach most of which could be classified as Type II semi-professional ad hoc collection for commercial outlet and not demand by local anglers.

Inevitably access to the bait stocks within this part of the Nature reserve was prohibited and there was rapid recovery of the population to normal levels once severe exploitation ended.

This case study reveals features in the life history and recruitment of the lugworm *Arenicola marina* that would encourage the development of management techniques in sutable areas. The juveniles of the lugworm *A. marina* occupy nursery areas physically separated from dense populations of adults (BEUKEMA & de VLAS, 1979; NEWELL 1948, 1949; OLIVE, 1993). Moreover in the area studied by OLIVE (1993) the adults exhibited a high degree of mobility and substantial numbers of adult worms migrated into the depleted areas from unexploited neighbouring tracts of beach within a few weeks of the ending of bait digging. The observations suggest that a system of progressive exploitation of areas alternating with periods of recovery from reserve areas could be an effective management technique for this species on extensive tidal sand flats.

Similar management techniques seem to be effective for the Type III commercial fishery for *Perinereis* and *Marphysa* in Korea where the tidal flats are divided into rectangular areas which are only dug over once each year (CHOI, 1985).

Whereas large extensive intertidal flats may be managed in this way such techniques are not appropriate for smaller pocket beaches. In such cases a judgement is required about the relative importance of bait collection, the requirements of other users of a beach and the importance of the beach fauna for conservation and educational purposes. Such value judgements can only be made by careful and sympathetic consideration at a local level.

Consideration must also be given to the population structure of the exploited species and important differences may be revealed between exploited and non-exploited populations. BRAFIELD & CHAPMAN (1967) demonstrate the dramatic change in weight frequency in a natural population of *N. virens* before and after the breeding season. These are semelparous worms and the data suggests that virtually all animals breed and die in the second or (fewer worms) third year of life. After the breeding season the population is dominated by I-group worms 3 and 11g in weight. The population structure of the worms caught by the summer Maine fishery is exactly comparable (CREASER *et al.*, 1983). In contrast the population of this species exploited by anglers in North wales (Menai Strait) was still dominated by much larger worms up to 60 g weight even after the breeding season (OLIVE, 1993)

Source : MNHN, Paris

and in this beach the worms appear to live much longer. The rate of entry to the fishery will be smaller and the OSY consequently much lower. The Menai Straits population could not therefore sustain a substantial fishery.

TABLE 1. — Principle Polychaete bait species, countries of origin and export destinations.
I. Production from wild stocks.

| Family and Species | Production Origin | Destination |
|---|---|---|
| **PHYLLODOCIDA** | | |
| **Nereidae** | | |
| *Nereis virens* | UK | UK |
| | USA (Maine) | USA, (CA,FL) France |
| | Ireland | UK, France |
| | | Italy, Spain. |
| | Netherlands | UK, France, Italy, Spain |
| *N. diversicolor* | | |
| *Perinereis cultrifera* | Italy | Italy |
| *Perinereis nuntia* | China | Japan |
| *P. brevicirrus* | Korea | Japan, USA, Europe |
| **Glyceridae** | | |
| *Glycera dibranchiata* | USA (Maine) | USA (Gulf and West coast states) |
| **Nephtyidae** | | |
| *Nephtys hombergi* | UK | |
| **EUNICIDA** | | |
| **Eunicidae** | | |
| *Marphysa sanguinea* | Korea | Japan, Europe USA |
| | Italy | Southern Europe |
| | Portugal | " " |
| *Marphysa leidyi* | Australia | |
| **Onuphyidae** | | |
| *Onuphis teres* | Australia | |
| **Lumbrinereidae** | | |
| *Lumbrinereis cf impatiens* | Italy | |
| **ARENICOLIDA** | | |
| **Arenicolidae** | | |
| *Arenicola marina* | UK, Netherlands | Europe |
| | France, Ireland | " |

Based on personal observations private market surveys and CREASER *et al.*, 1983, CHOI, 1985, GAMBI *et al.* (1994).

Studies of the population structure of exploited populations of bait worms suggest that only in relatively few areas are conditions suitable for a sustained fishery. The value of bait worms in world markets suggests that these fisheries alone are not able to meet all the demand.

## THE ROLE OF AQUACULTURE IN PROVISION OF BAIT SPECIES

The last 20 years has seen the phenomenal growth of aquaculture for crustaceans (LEE & WICKINS, 1992). Current FAO statistics suggest sustained development of this sector at about 18 % pa to give output by 1988 in excess of 200,000 metric tonnes. Could the development of aquaculture for bait species similarly alleviate the problems caused by the excess of demand over the Optimal Sustainable Yield of bait fisheries ? The problem is

Source : MNHN, Paris

particularly acute in Europe where by far the greatest bait fishery effort is directed at non-sustainable resources and where bait collection of Types I and II may service the greater part of the use of bait by leisure anglers.

Since one of the objectives of the development of an aquaculture system would be alleviation of environmental pressure it is important that the aquaculture should be fully intensive ie it should have the following elements :

i) Specific holding facility;
ii) Self contained brood stock and larval rearing system;
iii) Artificial diets.

Fully intensive aquaculture now contributes to Far East and European markets although the quantities being produced are small in relation to the market. In Taiwan approximately 25 tonnes of the nereid *Perinereis brevicirrus* are produced annually for export to Japan by fewer than 10 small farmers (CHEN, 1990) and small farms producing *Perinereis* are also found in southern Japan.

The development of polychaete culture in Europe has been driven by perceived commercial opportunity and a number of enterprises have been initiated notably in Netherlands and in the UK but there are no published accounts of their success, most are not thought to have established viable economic activity but one in NE England (see below) is now making a significant contribution (15 tonnes in 1992/3) to UK supplies of ragworm and expansion of this source material is expected.

A major problem in the aquaculture of *Perinereis brevicirrus* arises from the life history characteristics of this species. It is a semelparous annual; breeding occurs in late March and juvenile worms do not reach market size (minimum 1 g) until September. Since the principle market demand in Japan is between May and October these worms are only available for some two months of the season and can only represent a supplement to a market supplied by the natural fishery.

In 1979 the University of Newcastle upon Tyne (UK) began a research programme to select a suitable bait species for intensive aquaculture in Europe and to establish the operational parameters that would permit economic bait production. In 1986 the partly developed technology was transferred to the private sector for further development. This initiative has now established an economically viable production site for the bait worm *N. virens* on the North East Coast of England. Modern distribution methods mean that a single production site can supply all parts of the UK within 24 hrs and it is clear that a single production site can supply bait wherever there is demand.

Intensive aquaculture provides a means of supplying the specific market for live baits without recourse to predation of natural stocks and with little adverse environmental effect. The production system operating in NE England makes use of power station effluent and supplies the market throughout the year. The introduction of aquaculture in this market has been met with enthusiasm by the user and the specialised trade literature and is likely to expand its market share. Cultured products will inevitably compete with those derived from natural habitats and this is likely to have a stabilising influence on the market price for bait worms. This in turn will help to relieve those pressures on the natural environment that arise from the demand for bait in support of the leisure sea angling industry.

## RISKS ASSOCIATED WITH AQUACULTURE OF BAIT SPECIES

Like other emerging aquaculture businesses the aquaculture of polychaetes for use as bait must be perceived as a high risk business. There are fixed production costs associated with capital provision (brood tanks harvesting and packing facilities), food costs, costs of maintaining brood stocks and larvae, and risks associated with loss of stock to predators or pathogenens.

The Newcastle University/Seabait Ltd project has revealed the existence of previously unreported pathogens which can be controlled by correct management and husbandry procedures but which could cause severe losses in incorrectly designed production facilities.

One such condition provisionally named Tentacle Wasting Disease (OLIVE & MCGRATH, in prep) is associated with a flagellated vibrio cf *Vibrio parahaemolyticus*. This condition causes a progressive loss of the sensory organs of the head and eventually to abnormal behaviour and death. The condition can be induced in laboratory cultures by prolonged exposure to adverse conditions and can achieve epidemic proportions. A number of other specific pathogenic syndromes have been discovered including a specific anaemia and a condition resulting in external lesions. As in all forms of aquaculture the effectiveness of management techniques in avoiding conditions which

Source : MNHN, Paris

encourage the onset of pathogenenicity in organisms usually present but benign will be of paramount importance in the economic viability of systems of worm culture.

## OPPORTUNITIES ARISING FROM THE CULTURE OF BAIT WORM

The development of a viable system for aquaculture of bait worms in NE England establishes a new source of biological raw materials. The culture of bait generates a specific biomass with properties known to be valuable in the support of other forms of aquatic production. The worms have a high proportion of unsaturated fatty acids PUFA and the specific long chain PUFA known to be essential in the diets of marine crustacea are present (OLIVE *et al.*, 1992). These fatty acids contribute to the viability of artificially reared Penaeidae (LYTTLE *et al.*, 1990; MIDDLEDITCH *et al.*, 1979, 1980; KANAZAWA *et al.*, 1979) and a new source of materials in suitable form is likely to have a beneficial effect if incorporated into the diets of brood stock prawns.

The development of *Nereis virens* aquaculture establishes in effect mass cultures of worms of known parentage. JOHNS *et al.* (1989) have established that the growth rate of Nereidae can form the basis of a useful sediment bioassay. The value of this technique is currently under investigation in collaboration with Seabait Ltd. a private company who have developed techniques for cryopreservation of larvae. The growth of very young (4 - 6 setiger stage nechtochaetes) is easily quantifiable from segment proliferation rates and the growth rate of commercially available cryopreserved nechtochaetes (Seabait Ltd) is not significantly different from that of fresh unfrozen larvae under a variety of different test conditions when measured in this way (OLIVE & LANG, in prep).

The development of mass cultures of genetically uniform stocks and the application of cryopreservation techniques to juveniles should assist in the development of international sediment bioassay protocol.

## CONCLUSIONS

Polychaeta have their greatest economic value as bait in support of the leisure Sea Angling Industry. There appear to be relatively few places where a substantial commercial fishery can be sustained over decades. Consequently the price of suitable bait species is high and this leads to two consequences :

i) A large number of Sea Anglers dig their own bait from intertidal beaches;
ii) There is a substantial semi-professional exploitation of intertidal populations that frequently exceeds the sustainable yield.

In Europe there is evidence of increasing concern at the effects that such ad hoc bait digging has on beaches that are used for other recreational purposes or which lie in conservation areas.

The recent advent of commercially viable operations for the production of Polychaeta in self contained fully intensive aquaculture will help to alleviate price driven over exploitation of limited resources. At present cultured worms are perceived by some sections as offering definate advantages over the wild caught supplies and the average price of cultured worms in the UK may be higher than that of comparable worms taken from the wild.

There is a clear need for further studies of the dynamics of populations subject to different types of collection pressure. Some sites should be managed to sustain the Optimum Sustainable Yield. Local controls to regulate the exploitation of more limited stocks may be necessary especially where their is a clear conflict of interest.

## REFERENCES

BEUKEMA, J.J. & VLAS, J. de, 1979. — Population parameters of the lugworm *Arenicola marina* on the tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.*, **13** : 331-354.

BRAFIELD, A.E.& CHAPMAN, G., 1967 — Gametogenesis and breeding in a population of *Nereis virens*. *J. mar. biol. Ass. UK.*, **47** : 619-627.

CHEN, LO-CHAH, 1990. — *Aquaculture in Taiwan*. Fishing News Books: Oxford, 273 pp.

CHOI, I.H., 1985. — Lugworms - from harvesting to exporting. *Infofish marketing Digest*, **6/85** : 49-52.

Source : MNHN, Paris

CREASER, E.P., CLIFFORD, D.A., Jr., HOGAN, M.J. & SAMPSON, D.B., 1983. — A commercial sampling program for sandworms *Nereis virens* Sars, and bloodworms, *Glycera dibranchiata* Ehlers, harvested along the Maine coast. *NOAA Technical Report NMFS SSRF-767* : 1-56.

CREASER, E.P. & CLIFFORD, D.A., 1982. — Life history studies of the sandworm, *Nereis virens*, Sars in the Sheepscott estuary, Maine USA. *Fish. Bull.*, **80** : 735-743.

CREASER, E.P. & CLIFFORD, D.A., 1986. — Size frequency and abundance of subtidal bloodworms *Glycera dibranchiata*, (Ehlers) in Montswag Bay, Woolwich-Wiscasset, Maine. *Estuaries*, **9** : 200-207.

CROZ,L., WONG, L., JUSTINE, G. & GUPTA, M., 1988. — Prostaglandins and related compounds from the polychaete worm *Americonuphis reesei* Fauchald (Onuphidae) as possible inducers of gonad maturation in Penaeid shrimps. *Rev. Trop.*, **36** : 331-332.

CRYER, M., WHITTLE, G.N. & WILLIAMS, R., 1987. — The impact of bait collection by anglers on marine intertidal invertebrates. *Biol. Conserv.*, **42** : 83-93.

GAMBI, M.C., CASTELLI, C., GIANGRANDE, A., LANERA, P., PREVEDELLI, D. & ZUNARELLI-VANDINI, R., 1994. — Polychaetes of commercial and applied interest in Italy: an overview. *Mém. Mus. natn. Hist. nat.*, **162** : 593-601.

JACKSON, M.J. & JAMES, R., 1979. — The influence of bait digging on the cockle *Cerastoderma edule*, populations in North Norfolk. *J. App. Ecol.*, **16** : 671 - 679.

JOHNS, D.M., GINN, T.C. & REISH, D.J., 1989. — The effect of contaminated sediments on the growth of the Polychaete *Neanthes arenaceodenatata*. *Bull. Mar. Sci.*, **48** : 589.

KANAZAWA, A.TESHIMA, S. TOKIWA, S., KAYAMA, M.& HIRATA, M., 1979. — Essential fatty acids in the diet of prawn.II effects of docohexaenoic acid on growth. *Bull. Jpn. Soc. Sci.Fish.*, **45** : 1151 -1153.

KLAWE, W.L. & DICKIE, L.M., 1957. — Biology of the bloodworm *Glycera dibranchiata*. *Bull. Fish. Res. Bd., Canada*, **115** : 1-37.

LEE D. O'C. & WICKINS, J.F., 1992. — *Crustacean farming*. Blackwell Scientific Publishers : Oxford, 392 pp.

LYTLE, J.S., LYTLE, T.F. & OGLE, J.T., 1990. — Polyunsaturated fatty acid profiles as a comparative tool in assessing maturation diets of *Penaeus vannamei*. *Aquaculture*, **89** : 287-299.

MCLUSKY, D.S., ANDERSON, F.E. & WOLFE-MURPHY, S., 1983. — Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait digging. *Mar. Ecol. Progr. Ser.*, **11** : 173-179.

MIDDLEDITCH, B.S., MISSLER, S.R., WARD, D.G., MCVEY, J.B., BROWN, A., WARD, D.G. & LAWRENCE, A.L., (1979). — Maturation of penaeid shrimp: dietary fatty acids. *Proc. World Maricult. Soc.*, **10** : 472-476.

MIDDLEDITCH, B.S., MISSLER, S.R., HINES, H.B., MCVEY, J.B., BROWN, A., WARD, D.G. & LAWRENCE, A.L., 1980 — Metabolic profiles of penaeid shrimp; dietary lipids and ovarian maturation. *J. Chromatogr.*, **195** : 359-368.

NEWELL, G.E. 1948. — A contribution to our knowledge of the life history of *Arenicola marina* L. *J. mar. biol. Ass., UK.*, **27** : 554-580.

NEWELL, G.E., 1949. — The later larval life of *Arenicola marina* L. *J. mar. biol. Ass., U.K.*, **28** : 635-639.

OLIVE, P.J.W., 1993. — Management of the lugworm *Arenicola marina* and the ragworm *Nereis virens* (Polychaeta) in conservation areas: the importance of population structure and recruitment processes. *Aquati.Conserv. : Mari. Aquati. Ecosyst.*, **3** : 1-24.

OLIVE, P.J.W., BURY, N., COWIN, P.B.D. & SMITHARD, R.R., 1992. — Commercial production of Polychaetes for angling; implications for mainstream aquaculture. *Special Publication of the European Aquaculture Society*, **14** : 241-242.

SIMPSON, M., 1962. — Reproduction of the polychaete *Glycera dibranchiata*. *Biol. Bull. mar. biol. lab.*, Woods Hole, **123** : 396-410.

VAN den HEILIGENBERG, T., 1987. — Effects of mechanical and manual harvesting of Lugworms *Arenicola marina* on the benthic fauna of tidal flats in the Dutch Wadden Sea. *Biol. Conserv.*, **39** : 165-177.

Source : MNHN, Paris

# ABSTRACTS

# RÉSUMÉS

MORPHOLOGICAL AND GENETIC DIFFERENTIATION OF *HEDISTE DIVERSICOLOR* AND *NEANTHES SUCCINEA* POPULATIONS IN THE MEDITERRANEAN SEA. *ABBIATI, M.* — (Dipartimento di Scienze dell'Ambiente e del Territorio Università di Pisa, Via A. Volta 6, I-56126 Pisa, Italy). — *Hediste diversicolor*, like many other brackish water species, shows a high degree of morphological variability (MÜUS, 1967a). The variation in the numbers of paragnaths on the eversible proboscis is the most studied morphological parameter in *H. diversicolor* (MÜUS, 1967b; COGNETTI VARRIALE, 1973; BARNES & HEAD, 1977; BARNES, 1978; KHLEBOVICH *et al.*, GILLET, 1987, 1990; ABBIATI, 1989, 1991; ABBIATI & COGNETTI VARRIALE, 1990; HATELEY *et al.*, 1992). The observed interpopulation differences in *H. diversicolor* have prompted speculations that there may be isolated races in this species (MÜUS, 1967a). In order to obtain information on the level of intraspecific differentiation in *H. diversicolor* and to relate it to the level of interspecific differentiation, a study has been made of the morphological variation and genetic structure of three *H. diversicolor* and one *Neanthes succinea* populations, all collected along the Italian coasts. About one hundred individuals from each population were examined. The morphological character chosen for observation was the number of proboscis paragnaths, both in each group and on the whole. Differences among mean number of paragnaths present in each group of the proboscis were evaluated by Tukey's test to verify the level of significance. On this basis it was possible to recognise only two discriminant groups for all populations. In fact the eight proboscis groups are a useful tool for nereidids taxonomy, but they do not correspond to the functional unity of the proboscis (ABBIATI, 1989; HATELEY *et al.*, 1992). Looking at the total mean number of paragnaths of each population, significant differences between all populations were pointed out. Hierarchical relationships between all populations, based on the differences in the total mean number of paragnaths were defined. Genotypes were analysed by means of isozyme electrophoresis on cellulose acetate membrane. Fifteen enzyme systems were investigated; 17 and 21 loci were scored in *H. diversicolor* and *N. succinea* respectively. The percentage of polymorphic loci (0.99 cutoff criterion) and the mean number of alleles for the studied populations ranged from 23.5 % to 47.1 % and from 1.38 to 1.588 respectively. Comparison between *H. diversicolor* samples revealed that the populations are heterogeneous. Nei's identity and distance indices measure the relatedness of populations and species and are based on allelic variation at each locus (NEI, 1987). Genetic distance between *H. diversicolor* populations ranges from 0.272 to 0.351 and reveal that pairs of populations were significantly different from one another. The values found are those typically associated with local populations (NEI, 1987). Hierarchical relationships between all populations, based on genetic distance values were defined. The morphological and genetic distance between *H. diversicolor* and *N. succinea* was used as references for the respective scales. Comparison of the two dendrograms reveals a high degree of correspondence between the genetic and morphological differentiation levels. This result confirms the validity of the hypothesis proposed by many authors, based on morphological data, about phenomena of differentiation among *H. diversicolor* populations.

SPATIAL DISTRIBUTION OF POLYCHAETA IN HARD-SUBSTRATE IN THE NORTHERN LITTORAL OF CAP DE CREUS (SPAIN, NW MEDITERRANEAN). *ALOS, C.* — (Departament de Biologia Animal, Universitat de Barcelona, Diagonal, 645. 08028 Barcelona, Spain). — The polychaeta associated with hard substrate was studied in the northern littoral of Cap de Creus (NW Mediterranean) from 1981-1985, in the context of a general bionomic study of this zone (Programa de Bentos Cap de Creus). Starting from these data, it has been possible to establish a relationship between polychaeta populations and the environmental conditions which determine their spatial distribution. Ninety-one samples were studied from the main facies of this littoral, in which the three bionomic levels were included: surface facies with strong hydrodynamics (mediolittoral and upper infralittoral levels), photophilic algae biocoenose, *P. oceanica* beds, precoraligenous communities and coraligenous biocoenose. However, the high number of polychaeta species identified (235), the disparity in their appearance frequencies and the ambiguity in their ecological requirements make it very difficult to associate any species with a determinate bionomic level. In order to study the spatial distribution, different cluster analysis was made between samples and also between species, with the purpose of assigning to each group of species the ecological characteristics of substrate with which they are related. Results show that the high variety of facies appearing in hard-substratum does not correspond to characteristic populations of polychaeta. They are distributed according to microhabitats that are often the same in facies under different general conditions. The different populations

Source : MNHN, Paris

of polychaeta in this zone can be associated as follows: 1. Species from surface facies with strong hydrodynamics: *Lepidonotus clava, Eulalia viridis, Grubeosyllis vieitezi, Syllis prolifera, S. amica, Fabricia sabella.* 2. Species associated to calcareous concretions from calm environments: *Lysidice ninetta, Xenosyllis scabra, Syllis ferrani, Autolytus sardai, Opisthodonta morena, Polydora flava.* 3. Species from sciaphilic environments independently of substrate: *Harmothoe spinifera, Pholoe minuta, Sphaerosyllis pirifera, Pionosyllis lamelligera, Fabriciola* cf *baltica.* 4. Species from environments with a high degree of sedimentation (*P. oceanica* rhizomes and cavities could be filled up by sediment): *Parapionosyllis brevicirra, Ehlersia ferrugina, Exogone rostrata, Prionospio cirrifera, Kefersteinia cirrata, Sphaerosyllis brevicirra.* 5. Species with imprecise ecological requirements or with a high degree of cosmopolitisme. They are preferently located in the photophilic algae biocoenose and *P. oceanica* leaves: *Exogone naidina, Grubeosyllis clavata, Odontosyllis gibba, Pionosyllis serrata.*

GAMETES, FERTILIZATION AND DEVELOPMENT OF *PHERUSA* SP., AN ENDOLITHIC WORM (POLYCHAETA, FLABELLIGERIDAE). *AMOR, A.* — (Instituto de Embriologia Biologia e Histologia, calle 60 y 120 1900, La Plata, Argentina). — The polytelic worm *Pherusa* sp. is a gonochoric animal inhabiting hard substrates. Males and females could only be recognized during the reproductive season: the body of the males is white and that of the females green. In the laboratory, both sexes spontaneously spawn in seawater leading to normal fertilization. The eggs are green in colour and mesure about 140 µm in diameter. The spermatozoa are of primitive type. After fertilization the egg shows evident morphological changes of the surface and the pattern of the egg development is clearly spiral. The two blastomeres resulting from the first cleavage express differences in colour, AB is green and CD is white. All the egg pigment is concentrated in the small cell. The development is indirect comprising a larval pelagic stage, a pelago-benthic stage and a benthic stage. The pelagic and pelagobenthic stages develop in seven days and the larvae are lecitotrophic. A terminal organ appears in the pelagic larvae which becomes retractable and which secreted adhesive substances at the end of the pelago-benthic stage. Early in the pelagic development a dorsal depression appears indicating the location of the future anus. The mouth and the anus are both functional at the begining of the benthic life of the larvae. On the head, a pair of palps appear and there is an increased number of eye spots. The number of branchiae behind the head and the appearance of setae, different to those of the adults are the most notable. During all larval development new characters appear, with only the loss of the pelagic cilia of the larvae.

THE IMPACT OF FISHING HARBOUR CONSTRUCTION ON THE DENSITY OF BENTHIC POLYCHAETES OF THE COLEROON ESTUARY ON THE SOUTHEASTERN COAST OF INDIA. *AYYAKKANNU, K.* — (Centre of Advanced Study in Marine Biology, Annamalai University, Parangipettai, 608502 Tamilnadu, India). — A fishing harbour was constructed in the Colero on estuary (11°21'N, 79°50'E) on the southeastern coast of India during the years 1985-86 to accommodate about 300 fishing vessels. A quantitative benthic survey of polychaetes in this region was made in the years 1985-86 and 1986-87 during construction and after the fishing harbour started functioning and the data obtained on the population of these polychaetes was interesting for they throw light on the effect of dredging on these organisms. Eventhough the total number of species did not show great variations when compared to the earlier report from this region (JEGADEESAN, 1986), a reduction in the number of polychaetes was found. In earlier reports, 35 species of polychaetes were counted whereas 32 species was recorded during the construction and 29 species are recorded after the fishing harbour started functioning. The total number of polychaetes recorded was 174 ind. $m^{-2}$ during harbour activities; 224 ind. $m^{-2}$ after construction against 680 ind. $m^{-2}$ reported earlier. The following species were dominant: *Nephtys polybranchia, Ancistrosyllis constricta, Heteromastus similis, Lumbriconereis simplex, Ceratonereis costae* and *Prionospio pinnata.* However, these species though present, were found in a lesser number during and after the construction of the fishing harbour. The earlier report found *Ancistrosyllis constricta* as highly dominant species (68 ind. $m^{-2}$), but the present study revealed that the numerical abundance of *A. constricta* was poor compared to its associate species *Nephtys polybranchia.* From this, it is inferred that *A. constricta* proves to be a sensitive species and is unable to withstand even a slight disturbance of the substratum compared to *N. polybranchia.* The impact of dissolved oxygen concentrations, nutrients, salinity, temperature and sediment texture on the density of the polychaetes is discussed.

MONITORING THE GROWTH OF *SABELLARIA ALVEOLATA* IN THE FIELD. *BAMBER, R.N. & IRVING, P.W.* — (FAWLEY aquatic research laboratories Ltd, Marine & Freshwater Biology Unit, Fawley, Southampton S04 ITW, UK). — An extensive population of the reef-building worm *Sabellaria alveolata* (L., 1767) exists in the Severn Estuary, southwest Great Britain, predominantly sublittorally and concentrated around the 20 m isobath. Significant littoral colonies occur on the rocky foreshore of Hinkley Point, Somerset, at and below 2 m above Chart Datum.Two nuclear power stations, Hinkley Point 'A' and 'B', are sited on this headland. The discharge canal for the power station cooling water crosses the shore, allowing heated water from the outfall to flow across the rocks near low water mark. Water temperatures here are up to 10 °C above ambient. The individual units of *S. alveolata* reef growing within the flow of the cooling water effluent are substantially larger (by 5 to 10 times the volume) than reef units elsewhere on the shore. Hypotheses to account for this difference are: 1. More individual worms per unit area at the outfall. Analysis of quantitative core samples of outfall and control reefs showed that, if anything, the worms are less dense at the outfall site (8,000 ind. $m^{-2}$ compared to 13,000. $m^{-2}$ at control areas). 2. The worms at the outfall are not *S. alveolata.* Morphologically, the worms are *S. alveolata;* they are not *S. spinulosa* Leuckart, 1849. 3. Greater longevity of the reef units at the outfall. We do not know how to age a

Source : MNHN, Paris

*Sabellaria* reef; the worms are of identical size ranges at outfall and control sites. 4. Faster growth of worms or tubes at the outfall. Potential causes of differential growth are (a) a response to the greater water temperature at the outfall (although the worms themselves are no larger at the outfall site; however, winter growth or activity may be enhanced) or (b) increased input of material from the effluent flow (although at LWST turbidity is greater at the control site). We are currently investigating this possibility. The main work to date has been determining a suitable technique for non-destructive monitoring of reef growth in the field. We have tested four methods: 1. *In situ* volumetric displacement. Reef units were enclosed in a bottomless bin, lined with a plastic bag which was then filled with water; the weight of the water pressed the plastic closely to the reef, the bedrock and the bin sides. The difference between this volume of water and the volume of the bin was a measure of reef volume. In practice, errors on replication were up to 100 %! This method was rejected. 2. Frame-grid measurement. A cage of rigid plastic mesh supported around a tubular frame, and of known dimensions, was lowered around the reef, and measurements were made normally from each of the 5 cm interval intersections of the mesh to the reef face (top or side: the reef base is flat on the rock so can be reasonably assumed to be 0 cm above the frame base). A computer program calculated the volume of the subtended rectangular cuboid from the mean reef dimensions. Modelling tests on this technique suggested that it may underestimate the reef volume by ca 5 %; errors between replicates were commonly of the order of 10 %. This method was laborious, and was rejected. 3. Photography. In a manner not dissimilar to method two in its logic, photographs of marked reef units were taken from four sides (N, E, S, W) and the cross-sectional areas calculated. From these, the volume of the subtended rectangular cuboid was calculated. This procedure inevitably overestimates the volume. The data will be retested assuming the reef to be an oblate hemispheroid, but these results will still be prone to error owing to the irregular shape of the reef units. However, with the comparative ease of this technique, we are persisting with it in comparison to method four, to determine its suitability for more general use. 4. Displacement of detachable reef units. Individual reef units of *ca* 1.5 litres volume have been detached from the rock and mounted on plywood panels using an epoxy resin (WRA System 22). Previous laboratory tests had shown that this adhesive would cure under seawater, would adhere to the reef material after minimal drying, and when cured was stronger than the mucopolysaccharide adhering the reef grains. Larger base panels, 60 x 60 cm, were fixed to the shore bedrock using 10 cm silicon bronze screws. The panels bearing the reef units, after 24 hours curing in a rock pool on the shore, were screwed to these base panels. On each visit to the site, the units can be removed, their volume measured by direct displacement in a bin of sea-water, and they are then reattached to the shore to grow on. The 13 deployed reef units have survived intact for six months to date. The error margin between replicates (standard deviation) was 3.5 %. Not only is this method satisfactory and beginning to give results, it has allowed us to deploy control-site units at the outfall and vice versa. In conclusion, the technique of volumetric displacement of detachable reef units gives results of sufficient accuracy to detect growth. The complex initial preparation suggests that photographic analysis is worth further investigation, cross-calibrated with the displacement method, as it would prove convenient for use at other sites and involves less time on the shore.

THE ECOPHYSIOLOGY OF *HEDISTE (NEREIS) DIVERSICOLOR* O. F. MULLER (POLYCHAETA) IN THE BAIE DE SOMME, FRANCE. *Batten, S.D, Hawkins, L.E., Hutchinson, S., Desprez, M., Rybarczyk, H., Paterson, G.L., Lambshead, P.J.D. & Ducrotoy, J.P.* — (Southampton University Department of Oceanography, Southampton, SO9 5NH, U.K.). — *Hediste (Nereis) diversicolor* has a wide distribution in the intertidal areas of the Baie de Somme estuary. The polychaete has been sampled from two sites for a 12 month period, one site being relatively more disturbed. The population fluctuations have been studied from quantitative core samples sieved through a 0.5 mm sieve and fixed with 4 % formalin. Individuals were also frozen *in situ* in liquid nitrogen for physiological assay. The physiological components that have been measured are total lipid, carbohydrate and protein and the metabolites ATP, ADP, AMP, glucose, glycogen and creatine phosphate. Correlations between the population studies and the physiological assays have been made and provide much information on the reproductive cycles of this polychaete. Differences in the physiology and reproductive ability of the populations at the two sites have been noted. Further investigations to confirm the effects of the disturbance have been proposed.

SOME OBSERVATIONS FROM THE POLYCHAETA TO AID UNDERSTANDING OF THE RELATIONSHIP BETWEEN LARVAL DISPERSAL AND THE GEOGRAPHIC BOUNDARY OF SPECIES. *Bhaud, M. & Marcano, G.*—(Observatoire Océanologique de Banyuls, Laboratoire Arago, 66650 Banyuls-sur-mer, France). — It is not definitively clear whether species whose life history includes a planktonic larval stage will have as a consequence a larger distributional area than species lacking such a free drifting stage. The present contribution to this problem bears on five points: 1. definition of a non-biaised sample; two approaches are possible: the selection of isolated examples with well known area boundaries, preventing generalizing of results, or the selection of a large number of species correctly defined in terms of geographic distribution and reproductive strategies but occupying necessarily a heterogeneous environment which may obscure the relationship between larval dispersion and distributional area. 2. correct larval identification: a large amount of work is still needed as conclusions about geographic distribution drawn from family level identifications are not pertinent to the question of larval flow which must be examined at a lower systematic level. 3. modulation of larval life duration in terms of latitudinal position of the observation and larval behaviour with active or passive displacement in the face of physical oceanic structures are two additional elements determining the dispersal area of a species. 4. data on molecular population genetics of marine organisms must be discussed in order to include life style, population size, potential gene flow (larval

Source : MNHN, Paris

life) and environmental factors. 5: the model of a geographical boundary (*Mesochaetopterus minutus*, Chaetopteridae) shows the displacement between larvae and adults distribution, opens the possibility of pseudopopulations and probably renders to the benthic stage the key for the determination of the specific geographic range. It is concluded that distributional range is not accounted for by the inherent dispersal capacities related to larval type; such a conclusion raises the question of the meaning of a dispersal stage within the life cycle.

HIGH POLYCHAETE DIVERSITY IN THE DEEP SEA: HOW MANY SPECIES? *Blake, J.A. & Hilbig, B.* — (Science Applications International Corporation, 89 Water Street, Woods Hole, Massachusetts 02543, U.S.A.). — Recent studies on benthic infaunal communities in the western North Atlantic have revealed a remarkably high species diversity. Approximately 1600 species of benthic invertebrates were discovered in 550 quantitative box cores taken on the Canadian boundary to off South Carolina in depths ranging from 250-3,500 m. An equally rich infauna of approximately 600 species has recently been discovered from 67 box cores taken on the continental slope off northern California in depths of 550-3,100 m. In both of these studies polychaetes accounted for 45-48 % of all species, with 53 % of the Atlantic and 51 % of the California species being new to science. For some families from the western North Atlantic, the proportion of new species to known species was high: Capitellidae (29/35: 82 %), Chrysopetalidae (9/10: 90 %), Cirratulidae (33/40: 82 %), Dorvilleidae(28/34: 82 %), Hesionidae(11/15: 73 %), Orbiniidae (17/24: 70 %), Oweniidae (17/20: 85 %), Paraonidae (30/49: 61 %), Phyllodocidae (23/37: 62 %), Sabellidae (15/24: 62 %), Spionidae (62/80: 77 %), Syllidae (16/22: 72 %), and Terebellidae (21/25: 84 %). The total area sampled was 49.5 $m^2$ on the Atlantic slope and 6.7 $m^2$ in California. When considered in the context of the vast continental margins and ocean basins on the planet, the area covered by these samples is insignificant, but does provide an opportunity to estimate the potential richness of polychaete genetic diversity. In the most homogeneous region of the U.S. continental slope off Delaware and New Jersey, Grassle and Maciolek (1992) demonstrated that rates of species accumulation in 233 pooled box cores never leveled off. When taken in the context of the more heterogenous environments off New England and the Carolinas and the relatively small total surface that has been sampled in 550 box cores, the potential number of species of polychaetes actually present on the continental slope of the U.S. Atlantic is greatly underestimated. The data that are accumulating from the eastern Pacific from a fewer number of samples suggest that an equally high rate of species accumulation occurs with repeated sampling. These findings support the condusions of Grassle and Maciolek (1992) that the deep sea contains a vast reservoir of species richness. When taken in the context of the size of the unexplored continental margins and ocean basins, the high percentage of polychaetes in benthic assemblages, and rates of species accumulation with repeated sampling, it is possible that the total number of polychaete species in the deep sea may lie somewhere between 450,000 and 4 millions. A great genetic reservoir of polychaete diversity thus occurs in the deep sea. Some species have been determined to have broad geographic and depth distributions and this may serve to reduce these estimates. Nevertheless, even with a 50 % reduction, the remaining totals are far in excess of the numbers of presently known polychaete species.

BENTHIC MACROFAUNA AND POLYCHAETES FROM AN EXPERIMENTAL AREA IN THE DEEP PERU BASIN (SE PACIFIC). *Borowski, C.* — (Zool. Inst. & Mus. Univ. Hamburg, Martin-Luther-King-Pl. 3, D-2000 Hamburg 13, Germany). — During the Disturbance and Recolonization Programme (DISCOL) of the Institut fur Hydrobiologie und Fischereiwissenschaft (IHF-Hamburg, Germany) a disturbance experiment was operated on the bottom of the Peru Basin, in a water depth of 4,150 m. Several boxcore samples were taken before and after the disturbance in a circular experimental area with a diameter of two miles. The samples were sieved with 1,000 µm and 500 µm mesh size and investigated quantitatively for sediment-dwelling macrofauna. Preliminary results from some selected undisturbed samples show that the majority of the infaunal animals is of a very small size that passes through the 1,000 µm mesh. More than 70 % are living in the uppermost 2 cm of the sediment, only about 5 % being found underneath 5 cm depth. The polychaetes make up the major element of the macrofaunal community (about 50 % of all animals), followed by isopods and tanaids (about 15 % each). Within the infaunal Polychaetes 78 species belonging to 34 families occurred. The highest numbers of species were found within the families Opheliidae (9), Syllidae (7), Spionidae (6) and Cirratulidae (5). Only four species were abundant enough to appear in nearly every sample (one Pilargiidae, one Paraonidae, two Spionidae); most of the others are rare. The hard substratum of the manganese nodules represents another common polychaete habitat. A total of 17 species (one Ampharetidae, 14 Serpulidae and two Spirorbidae) living on the nodule surfaces could be distinguished. Additionally, 12 infaunal species were found living in the nodule crevices. Six of them did not occur in the sediment samples.

*PRIONOSPIO CASPERSI* LAUBIER (POLYCHAETA, SPIONIDAE) IN THE BLACK SEA: ECOLOGICAL NOTES. *Britayev, T.A., Castelli, A., Aksiuk, T.S. & Severtzov, A.N.* — (Institut of Evolutionary Animal Morphology and Ecology, Russian Academy of Sciences, Moscow, 117071, Russia). — Numerous specimens of the spionid polychaete *Prionospio caspersi* Laubier, were found in the benthic samples from Kapsel Bay (on the southeastern coast of Crimea). This was the first record of this species in the Black Sea. *P. caspersi* is very abundant in sandy or silty sand communities at depths of 9 to 23 m in which the bivalve *Chamelea gallina* predominates. We have studied the density of population and frequency of occurrence of this species from 1986 to 1989. Density varied seasonally. It was highest in Spring (up to 730 ind. $m^{-2}$) and fall decreased in August-September (to 96 ind. $m^2$). The maximum density was about 2,440 ind. $m^2$. The frequency of

Source : MNHN, Paris

occurrence in grab samples varied from 53.6 % to 100 % and also declined at the end of summer. This data was in agreement with that of AMBROGI concerning the annual life cycle and the beginning of settlement in the last half of summer. In 1989, *P. caspersi* completely disappeared from benthic samples from Kapsel Bay and was replaced, as the dominant species, by the paraonid *Aricidea (Allia) claudiae* Laubier.

PELAGIC POLYCHAETES FROM EL HIERRO (TFMCBM/91) IN THE CENTRAL-EAST ATLANTIC. *BRITO, M. C., NUNEZ, J. & BARQUIN, J.* — (Departamento de Biologia Animal (Zoologia), Universidad de la Laguna, 38206 La Laguna, Tenerife, Canary Islands, Spain). — Seventeen quantitative plankton samples from the island El Hierro (Central-East Atlantic Ocean) have been studied; in sixteen of them pelagic polychaetes have been collected. From a total of one hundred and one specimens, seventeen species of polychaetes were identified. One of these unidentified species, genus and family. Furthermore, five species were recorded for the first time in the Canary Islands *(Tomopteris nationalis, T. euchaeta, Lopadorrhynchus henseni, Vanadis minuta* and *Rhynchonerella petersi)*. Details are given about the density and frequency of the species, as well as a biogeographical analysis of them.

TRANSPORT AND SURVIVAL OF LARVAL POLYCHAETES IN BALLAST WATER OF OCEAN-GOING VESSELS HEADED FOR THE GREAT LAKES. *BYERS, S.C., LOCKE, A. & BHAUD, M.* — (Royal Ontario Museum, Department of Invertebrate Zoology, 100 Queen's Park, Toronto, Ontario, MSS 2C6, Canada). — Great Lakes Ballast Water Control Guidelines were established by the Canadian Coast Guard in 1989 to minimize introductions of exotic species into Great Lakes ecosystems. Such introductions, including the zebra mussel, *Dreissena polymorpha*, have been attributed to intercontinental transport in the ballast water of ocean-going vessels. According to the guidelines, ships destined for the St. Lawrence Seaway and Great Lakes voluntarily replace all water ballast taken on in fresh or brackish areas with mid-ocean water. The rationale for mid-ocean exchange is that theoretically the freshwater and coastal organisms would be flushed out or killed by the water from the high seas. A study was launched in 1990 to a) determine the compliance of inbound ocean-going vessels with ballast water exchange guidelines, and b) to establish the effectiveness of open-ocean exchange of ballast water in reducing or eliminating the presence of limnetic and estuarine organisms in ballast water discharged in the Upper St. Lawrence River and Great Lakes. Compliance of vessels with the guidelines was 95 % (all vessels) or 89 % (excluding vessels not carrying ballast water). Effectiveness of mid-ocean ballast water exchange in eliminating live freshwater zooplankton from ships originating in freshwater ports was estimated to be 67 %. Twelve phyla of zooplanktonic organisms were identified from ballast tank samples, numerically dominated by copepods, cladocera and rotifers. Polychaeta, though not significant numerically, were represented by pelagic larval stages of the families Spionidae (*Polydora, "Polydora* complex", *Spiophanes)*, Phyllodocidae *(Eteone,* and sub-family Phyllodocinae), and Cirratulidae. Successful introduction and dispersal of a species to the Great Lakes are most likely for species that are eurytopic, fecund, and vagile. The last two attributes apply to most marine species of Spionidae, Phyllodocidae and Cirratulidae. The first attribute may be characteristic of certain species of Spionidae. No representatives of the two most numerically abundant freshwater polychaete families (Nereidae, Sabellidae) were encountered in this study. It is feasible, however, that such polychaetes could tolerate the mixohaline properties associated with the flushing or exchange of ballast water and flourish on introduction into the Great Lakes ecosystems, though no significant ecological threat would be expected. Brackish water polychaete families (19), of which Spionidae and Cirratulidae are representative, may survive the ballast water exchange but not necessarily subsequent limnetic conditions. Marine species taken on in the ballast water from the high seas would pose little threat of introduction.

BENTHIC POLYCHAETOUS ANNELIDS OF OGNINA BAY (EASTERN SICILY, ITALY). *CANTONE, G. & FASSARI, G.* — (Mollica E Dipartimento di Biologia Animale, Università di Catania, via Androne, 81-95124 Catania, Italia). — The Polychaetous Annelids of Ognina bay have been studied. Forty-three stations, along eight transects perpendicular to the coast, at depths from 30 cm to 112 m, have been sampled. Twenty-eight stations were located on rock surfaces and samples were collected by scraping quadrants of 25 x 25 cm; on soft substrates a "CHARCOT-PICARD" dredge (50 $dm^3$ capacity ) was used. One hundred and thirty five species were collected, leading to the recognition of typical biocenoses and "facies of transition". Shannon's index, redundancy and equitability for each station have been calculated, whereas to test the similitude between the stations, we made use of Kulczynski's index. Three different types of population are recognizable - photophilic and sciaphilous populations are found on hard substrates, and a third type exists on soft substrates. Following examination of the samples, no evidence of pollution has been found.

SPATIAL DISTRIBUTION OF AN EPITOKOUS NEREID SPECIES IN AN INTERTIDAL ESTUARINE: THE ROLE OF THE HYDRODYNAMIC. *CARON, A., OLIVIER, M., DESROSIERS, G., HUDIER, E. & RETIÈRE, C.* — (Centre d'Océanographie, Département d'Océanographie, Université du Québec à Rimouski, 310 allée des Ursulines, Rimouski, Québec, Canada G5L 3A1). — From observations made in a sheltered inlet ("Anse à l'Orignal", lower St Lawrence estuary, Canada), we discuss the influence of hydrodynamic processes on the spatial distribution of a community of *Nereis virens*. Data obtained during this study revealed an edaphic segregation between sexually mature and immature individuals. This observation has been correlated with the sediment thickness. Highest densities of the nectochaete larvae occured at the uppermost part of the intertidal flat in which we observed a weak flow regime associated with fine particules deposit. Highest adult densities were found in the diffusion area of waters ebbing away from the bay. These results suggest that during the short

Source : MNHN, Paris

period of time of their pelagic life the larvae will be transported in the water column and settle in weak flow regime areas. After a growth period of three or four years individuals will reach their sexual maturity and begin a migration toward the lower part of the intertidal flat. Despite their swimming ability it seems that migration is a passive one and is mainly controlled by hydrodynamics processes.

SEDIMENT PORE-WATER TOXICITY TESTING WITH THE POLYCHAETE *DINOPHILUS GYROCILIATUS*. *Carr, R.S.* — (U.S. Fish and Wildlife Service, NFCR Field Research Station, CCSU, Box 315, Corpus Christi, Texas 78412, USA). — The results of recent studies suggest that it is the contaminants associated with pore (interstitial) water that control the toxicity of contaminated sediments. Studies with the polychaete *Dinophilus gyrociliatus* exposed to pore water obtained from contaminated sediments demonstrated highly significant correlations between reproductive suppression and the concentration of a variety of contaminants in the sediments including polycyclic aromatic hydrocarbons, pesticides, and various trace metals. The short life-cycle of *D. gyrociliatus* allows effects on reproduction to be determined after a one-week exposure. Recent studies have focused on (1) optimizing pore-water collection procedures to minimize the loss of contaminants during the extraction process, and (2) comparing the *Dinophilus* life-cycle test with other sensitive toxicity tests (e.g., fertilization, morphological development, and genotoxicity assays with the sea urchin, *Arbacia punctulata*). Results to date indicate that the sensitivity of the polychaete test is comparable to test results with the sea urchin assays and other toxicity tests with sensitive life-stages of sensitive species. These pore-water toxicity tests are now being used routinely in large sediment surveys throughout the United States to determine the quality of the marine and estuarine sediments.

TEMPORAL VARIABILITY OF BENTHIC MACROFAUNA: THE DYNAMICS OF *PARAPRIONOSPIO PINNATA* (EHLERS) (POLYCHAETA, SPIONIDAE) AT BAHIA CONCEPCION, CHILE. *Carrasco, F.D.& Gallardo, V.A.* — (Departamento de Oceanologia, Universidad de Concepcion, P.O Box 2407, Concepcion, Chile). — Temporal oscillations of numerical density of macrobenthic organisms were studied on Concepcion Bay, Central Chile, during a 3-year survey of the infauna at a 22 m deep fixed station. A relatively low species richness (40 species) but with a high ecological resilience were observed. The spionid *Paraprionospio pinnata* (Ehlers) conformed the most important population in the 0.5 mm sieved muddy sediments of the area both in terms of its contribution to the density (ca. 97 %) and biomass. This high ecological dominance explain the low species diversity values encountered for this macrofaunal assemblage. The polychaete *Cossura chilensis* ranked second far behind. The abundance curve for *P. pinnata* showed at the beginning of the study period, early 1988, medium to high numerical abundances with a maximum peak in July 1988 (76,459 ind. $m^{-2}$). Thereafter a sharp decrease in density was observed, until a minimum of only a few specimens was reached in January 1989. From this time the worms practically dissapeared from the samples, situation which persisted for throughout the year 1989 till March 1990. This defaunation was also observed with the rest of the macrofaunal species. In May 1990 the numerical density of the *P. pinnata* population began to recover, reaching a maximum peak (63,694 ind. $m^{-2}$) in November 1990 to decrease again towards the end of the study period. The shape of abundance curve, and thus temporal variability, of *P. pinnata* is not to be expected according previous studies, specially in cases of the dramatic defaunations reported. We suggested that the 1989 defaunations were induced by the action of long and persistent (several weeks) very low levels of bottom water dissolved oxygen concentration. These hypoxias, which are common but aperiodic and of short duration in the area, probably caused the die of organisms and precluded larval recruitment.

EFFECTS OF WATER MOVEMENT DISTURBANCE ON POLYCHAETE STRATIFICATION IN INFRALITTORAL MUDDY BOTTOMS. *Castelli, A. & Prevedelli, D.* — (Dipartimento di Biologia Animale, Università di Modena, Via Università 4, I-41100 Modena, Italy). — According to well known patterns the benthic distribution is influenced by quality and intensity of hydrodynamics; however, knowledge about the stratification of infralittoral muddy bottom macrobenthos under high hydrodynamic conditions is scanty. In order to study this problem, the polychaete stratification dynamics have been analyzed in an annual cycle, with parallel recording of water motion as an index of hydrodynamic energy. The sampling site is located on muddy bottoms in an area facing the Po River delta (Northern Adriatic Sea), at 10 m depth. Samples have been collected by a box-corer during six surveys performed between september 1989 and september 1990. Each sample was splitted in four vertical layers: 0-2 cm, 2-5 cm, 5-10 cm, and 10-20 cm. The hydrodynamic conditions clearly influence the extension of the layer colonized, considering both the entire polychaete assemblage and single groups of species identified according to their trophic and ecological requirements. A total of 47 species have been collected. Individual abundance and species richness usually sharply decrease between the first and the second layer. The dominant species in the superficial layer are small-sized surface deposit-feeders such as the spionids *Polydora flava* and *Prionospio cirrifera* and the paraonids *Aricidea assimilis, A. claudiae,* and *Levinsenia gracilis*. In the deepest layer tubicolous species of great dimension dominate (i.e. *Maldane sarsi* and *Melinna palmata).* Deep burrowers, such as *Nephtys incisa,* are uniformely distributed along the whole sediment profile. A preliminary consideration on the collected data pointed out that the substratum thickness colonized by small-sized surface deposit-feeders tends to increase after the summer and early autumnal calms and tend to decrease after the storm periods (winter and spring). The assemblage colonizing the deepest layer (below 10 cm), however, did not vary significantly. Furthermore, after the period of stronger storms, abundance of the smaller specimens colonizing the superficial layer significantly decreases,

Source : MNHN, Paris

probably in relation to the substantial resuspension of the superficial layer of the sediment. Role of hydrodynamics in respect to the strategy of the recorded species and in structuring the polychaete assemblage is also discussed.

CENSUS OF POLYCHAETES OF THE ITALIAN COASTS. G.P.I. (Gruppo Polichetologico Italiano). *CASTELLI, A.*— (Dipartimento di Biologia Animale, Università di Modena, Via Università 4, I-41100 Modena, Italy). — At the Polychaete Conference of Long Beach (California), the G.P.I. (Gruppo Polichetologico Italiano) presented a programme, co-ordinated by A. CASTELLI, devoted to a census of the species recorded so far along the Italian coasts. This programme is a preliminary part of a large scale international project (promoted by I.C.S.E.M. and co-ordinated by G. BELLAN) devoted to studying the polychaeto-fauna of the Mediterranean Sea. The first results of this census, concerning families and species recorded (779 species belonging to 68 families) and first dichothomic keys available (Paraonidae - by A. CASTELLI - with 24 species belonging to seven genera), were summarized in a contribution presented at the Long Beach Conference. Successively, several other contributions on this topic became available; in particular those concerning Flabelligeridae, Poecilochaetidae, Hesionidae, Spionidae, Sabellidae, Capitellidae, and Pilargidae. The contents of these new reports may be summarized as follows: the census of Flabelligeridae (by A. CASTELLI) points out the occurrence of eight species belonging to six genera. The census of Poecilochaetidae (by G. CANTONE) points out the occurrence of three species all belonging to the genus *Poecilochaetus*. The census of Spionidae (by C. LARDICCI) points out the occurrence of 39 species belonging to 15 genera. The census of Sabellidae (by A. GIANGRANDE) points out the occurrence of 45 species belonging to 20 genera and three subfamilies. The census of Capitellidae (by M.F. GRAVINA & A. SOMASCHINI) points out the occurrence of 20 species belonging to 12 genera. Lastly the census of Pilargidae (by A. CASTELLI) points out the occurrence of six species each belonging to different genera. In addition, the contribution on Syllidae (which is by far the largest family along the italian coasts), Nepthyidae, Serpulidae, Spirorbidae, Nereididae, Aphroditidae, Polynoidae, Polyodontidae, and Sigalionidae are in press.

REPRODUCTIVE BIOLOGY OF *AMPHITRITE* SP. (POLYCHAETA, TEREBELLIDAE) IN TAIWAN. *CHEN, C.-P. & CHEN, R.B.* — (Institute of Zoology, Academia Sinica, Taipei, Taiwan 115, Republic of China). — *Amphitrite* sp. is distributed commonly in the intertidal sandflats of the west coast of Taiwan (and is probably a new species, Hutchings, pers.comm.). Adult worms are about 10 cm in length. Worms live in "U" shaped tubes, which aggregate closely to form a cluster of about 10 cm in diameter. Field samplings were conducted monthly from September 1990 to August 1991 at Hsin-Chu (N 24°50'; E 120°54'), Taiwan. Among 660 intact individuals collected, 141 were male, 111 female and 408 sex-indeterminable. Worms are dioecious with a sex ratio of 1: 1. Males had an average of 105.8 (sd, 16.2) segments; females 103.6 (sd, 15.2). The smallest male had 74 segments and the smallest female had 66 segments. The septa between segments is incomplete. Mature ova are 120 to 180 µm in diameter, and fecundity is 55,000 (sd, 25,000). Seasonal change of the incidence of sexual determination and oocyte-size distribution pattern reveals that spawning may occur in both spring and fall. Aulophore larvae of less than 10 segments having one tentacle within a hyaline tube were found benthically in association with tubes of adults. Juvenile recruitment occurred mainly during the summer with a minor recruitment in late spring.

NERVOUS SYSTEM OF *PSEUDOPOTAMILLA RENIFORMIS* BRUGUIERE AND SOME OTHER SABELLIFORM POLYCHAETES. *CHUGHTAI, I. & KNIGHT-JONES, E.W.* — (School of Biological Sciences, University of Wales, Swansea, U .K.). — Most emergent tubes of *Pseudopotamilla* are so orientated that the dorsal side of the expanded crown faces away from the substratum. This crown forms a bilaterally symmetrical fan, with most of the radiolar compound eyes facing dorsally and thus towards incident light and the main incoming water current. The nerves from the crown connect dorsolaterally with the brain, which is much thicker than the segmental commissures. Above it two horn-shaped lobes flank the dorsal groove and contribute pedunculate processes. Near these paired giant axons originate, decussate and run back in the circumoesophageal connectives. On each side a lateral lobe contains a cerebral eye, but the anterior part of the ventral nerve ladder shows no cephalisation. The intersegmental positions of the ventral ganglia may be associated with the septal attachments of the chaetal musculature; they also leave room for segmental development of the ventral gland shields, which are particularly thick in this species. Each ventral cord is in close contact with a paramedial group of longitudinal muscle fibres, and about half the cross-sectional area of each cord is occupied by a giant axon, throughout most of the thorax and anterior abdomen. These axons are joined via some transverse commissures and each is linked to many neurones of various sizes. More posteriorly, where the coelom is full of sex products and the muscles are reduced to a thin layer, giant axons are reduced or absent. The peculiarities of sabellid nervous systems will be compared with those of related forms and other polychaetes.

MOLECULAR CHARACTERIZATION OF A METALLOPROTEIN OF *HEDISTE (NEREIS) DIVERSICOLOR* (ANNELIDA POLYCHAETA). ITS PHYLOGENIC INTEREST. *DHAINAUT, A., SALZET-RAVEILLON, B., DEMUYNCK, S. & DHAINAUT-COURTOIS, N.* — (Université de Lille I, Laboratoire de Phylogénie Moléculaire des Annélides, URA CNRS 148, 59655 Villeneuve d'Ascq Cedex, France). — Physiological parameters able to provoke the synthesis and releasing of the metalloprotein MP II seem to be various: metallic exposition, bacteria agression, osmotic stress,...In order to precise how modulated is the expression of genes encoding MP II, a cDNA probe was produced. From the MP II amino acid sequence known, two oligonucleotidic probes were synthetized. Using PCR (Polymerase Chain Reaction), a 250 bp fragment corresponding to

Source : MNHN, Paris

the exon encoding MP II was obtained and has allowed us to realize *in situ* hybridation experiences. First results reveal the presence of a genic expression in cœlomic cell clumps and in some muscles. Quantitative estimation of this expression was studied by mRNA extraction and Northern Blotting. Characterization of the molecule MP II is interesting with regard to phylogenic considerations. MP II shares high similitudes with hemerythrins and myohemerythrins of sipunculids described in the litterature. Moreover, works done in our laboratory by other people have shown the existence of related molecules in oligochaete and achaete species. Evaluation of its distribution in other invertebrate phyla is now under progress. Results in that field would be of importance for the understanding of phylogenic relationships between some invertebrates.

RESPONSE OF ESTUARINE BURROWING INVERTEBRATES TO METALLIC POLLUTION. *Dhainaut-Courtois, N., Septier, F., Romont, R., Demuynck, S. & Dhainaut, A.* — (Université de Lille I, Laboratoire de Phylogénie Moléculaire des Annélides, URA CNRS 148, 59655 Villeneuve d'Ascq Cedex, France). — Estuarine burrowing species constitute good models to appreciate biological impacts of micropollutants having a continental origin. Among the available species at the different sites studied by ourselves in the North of France, much attention was paid to the particularly abundant species *Hediste (Nereis) diversicolor* (Annelida, polychaeta) having all the criterias required to serve as a bioindicator. The aim of the ecoepidemiological studies was to check correlations between the metallic content of sediments and animals. In addition to these *in situ* studies, experimental laboratory works were carried out to detect interactions between metals and physical parameters (pH, salinity, t°...) able to modify the concentration factors. Moreover, cytopathological effects due to several metals were checked by means of electron microscopy. By atomic absorption spectrophotometry, chromatography and electrophoresis, two iron-containing proteins called MP I and MP II able to bind cadmium ions were detected. Results which were obtained by biochemical and ultrastructural methods and by radioautography using $^{109}Cd$ appear to indicate that the high molecular weight protein (MP I) would be the extracellular hemoglobin. The latter protein (MP II) which is not a metallothionein was found to be able of bacteriostatic activities. This protein, close to 13,5 kDa has been sequenced and revealed high homologies with two respiratory proteins: hemerythrin and myohemerythrin. Using poly- and monoclonal antibodies raised against MP II, a possible site of synthesis was found to be granulocytes cells (G I). To conclude, MP II protein seems to play different roles: possible intervention in a detoxication process by its capacity to bind toxic heavy metals; bacteriostatic activity(ies) occurring by iron deprivation of bacterias. At the moment, the role of MP II in the transport of dioxygen remains uncertain.

POLYCHAETES FROM THE ISLAND OF BARBADOS, W.I. SETTLEMENT AND SUCCESSION. *Diaz, V.* — (Dep. Ecologia, CICESE, P.O. Box 434843, San Diego, CA 92143, U.S.A.). — Settlement and temporal succession of organisms on coral plates (*Montastrea annularis*) were examined at two fringing reefs on the west coast of Barbados: Spring Garden (polluted area) and Six Men's (non disturbed area). Two series of coral plates (60 $cm^2$) were fixed at 10 m depth. Series A was immersed the 28/02 and series B the 8/05/1990, they were constituted by 15 and 12 plates respectively. It is clear that the most abundant animal colonisers are Polychaetes. The first animals to colonize the bare surfaces were polychaetes and crustaceans (amphipods). On upper surfaces pioneer polychaetes are represented in series A by *Nereis* sp, *Glycera abranchiata, Exogone gemmifera* and some Syllidae in S. Garden whereas in S. Men's we have *Polydora* sp, *Ceratonereis mirabilis, Syllis* sp. and some *Filograna* sp. In B we collected *Dorvillea cerasina, Polyophtalmus pictus*, Amphinomidae and some Cirratulidae in the polluted reef area and in S. Men's: *Salmacina* sp, *Polycirrus medusa* and some Nereidae. On lower surfaces, encrusting colonial organisms were important in the initial colonization process (ascidians, bryozoans). Serpulidae was the dominant family of polychaeta (*Salmacina* sp, *Pseudovermilia occidentalis, Hydroides mucronatus, H. mongeslospesi, H. parvus, H. bispinosus, Pomatostegus* sp), followed by Spirorbidae (*Spirorbis epichysis, S.* cf. *knightjonesi*,...), we also found some Nereidae (*Ceratonereis mirabilis*). The most abundant polychaetes on upper surfaces were nereids, syllids, terebellids and spionids in Series A, and eunicids, syllids and capitellids in series B. On lower surfaces were serpulids, spirorbids, spionids and syllids in series A and serpulids, spirorbids and syllids in B. Algal films seem important to induce polychaete settlement. Globally, there is a trend towards increasing abundance over time. Diversity and abundance were higher on the polluted area. Diversity was higher on upper surfaces, whereas densities were higher on lower surfaces. A great proportion of Polychaetes were deposit-feeders exploiting the abundant organic matter (2 to 24 mg sed. $d^{-1}$. $cm^{-2}$ in S.Garden, 0.5 to 7 mg sed. $d^{-1}$. $cm^{-2}$ in S.Men's). In conclusion, Polychaetes play an important role in the colonization process in hard tropical bottoms. The pattern of early colonization on the reef is different for surfaces exposed to light and sedimentation than it is for surfaces protected from these factors. The two courses of colonization create different ecological assemblages.

LIFE CYCLE AND PRODUCTION OF POLYCHAETE SPECIES IN THE AIGUAMOLLS SALT MARSH (ROSES, GIRONA, NE SPAIN). *Dueso, A. & Sarda, R.* — (Centre d'Estudis Avançats de Blanes, Cami de Santa Bàrbara s/n, E-17300, Blanes, Girona, Spain). — Mediolittoral and infralittoral muddy and silty sand sediments in brackish waters of the Mediterranean Sea are characterized by the presence of a typical macroinfaunal assemblage dominated by the polychaetes *Hediste diversicolor* and *Streblospio shrubsolii*, the bivalve *Cerastoderma edule* and the amphipods *Corophium* ssp. Although abundant data of densities can be found in the literature, the dynamics of this particular assemblage is poorly known. Benthic macroinfaunal populations in several areas (five stations, three replicates by station) of Els Aiguamolls Salt Marsh (Roses, Girona, NE Spain) has been monitored from April 1991 to date using a corer (3.5 cm in radius). Samples

Source : MNHN, Paris

were processed through 500 µm mesh and the mud going through the mesh was sorted under binocular microscope to count the smaller size fraction of the different populations. To calculate biomass of the species, digitized lengths of all specimens were recorded using a computer aided programme. Regressions of length vs dry weight were calculated to estimate biomass from length. We employed ELEFAN software to analyze growth and production of the different cohorts observed. In this paper we presented the population structure, seasonal dynamics and production of the two dominant polychaete species: *H. diversicolor* and *S. shrubsolii* in tidal creeks of the salt marsh during the first year. Both species shows an extended spawning season with constant recruitment through the year although pe aks of recruitment were detected in early winter. Abundance data ranged from 2,036 ind. $m^{-2}$ in August to 16,305 ind. $m^{-2}$ in December (average of 11,798 ind. $m^{-2}$) for *S. shrubsolii,* and from 390 ind. $m^{-2}$ in September to 14,898 ind. $m^{-2}$ in January (average of 5,145 ind. $m^{-2}$) for *H. diversicolor.* Biomass data ranged from 0.63 g. $m^{-2}$ in August to 5.22 g. $m^{-2}$ in December (average of 2.50 g. $m^{-2}$) for *S. shrubsolii,* and from 0.11 g. $m^{-2}$ in November to 7.41 g. $m^{-2}$ in July (average of 2.83 g. $m^{-2}$) for *H. diversicolor.* Population abundances peaked during winter and there was a sharp decrease in densities through summer. The total benthic secondary production in the creeks for these two species, estimated as increases in biomass fron one sampling date to the next, was 17.97 g. $m^{-2}$ (9.58 g. $m^{-2}$ for *H. diversicolor* and 8.40 g. $m^{-2}$ for *S. shrubsolii).* P/B ratios for these two species were estimated as 3.38 for *H. diversicolor* and 3.36 for S. *shrubsolii.* The results found in Els Aiguamolls Salt Marsh are compared with data from temperate zones of the Mediterranean and Atlantic Coast.

FEEDING BEHAVIOUR AND FUNCTIONAL MORPHOLOGY OF THE INTROVERT AND DIGESTIVE SYSTEM OF *MYZOSTOMA CIRRIFERUM* ( MYZOSTOMIDA). *Eeckhaut, I., Dochy, B. & Jangoux, M.* — (Université de Mons-Hainaut, 19 avenue Maistriau, 7000 Mons, Belgium). — Myzostomids are poorly known annelid-related invertebrates associated with echinoderms, particularly comatulid crinoids. One of the interests that the myzostomids get from the symbiosis with the comatulids is the alimentary supply furnished passively by the host: most of the myzostomids feed on alimentary particles catched by the host. However, except anecdotal observations, very little is known of both their feeding behaviour and the structure of their digestive system. For this work, we studied the symbiotic pair *Antedon bifida* (Pennant, 1777) (Crinoidea) and *Myzostoma cirriferum* Leuckart, 1836 which were collected by Scuba diving at Morgat (Brittany, France). All postmetamorphic stages of *M. cirriferum* feed on alimentary particles carried by the ciliary current of the host's ambulacral grooves. They feed preferentially at the level of the pinnular grooves (myzostomids of 0.07 to 0.6 mm long) or the arm grooves (myzostomids of 0.6 to 1 mm long) or the calycinal grooves (myzostomids of 1 to 2.4 mm long). The digestive system of *M. cirriferum is* made of a pharynx included in an antero-ventral protrusive introvert (the mouth opens at the apex of the introvert), a stomach from which start blind digestive caeca, and an intestine which opens to the exterior by a postero-ventral anus. The mouth is surrounded by a sensory lip and four pairs of sensory papilla. The pharyngial lumen is bordered by a cuticuled pseudostratified myoepithelium which is surrounded by a highly developed musculature. The rest of the digestive system is made of a non-cuticuled monostratified epithelium surrounded by a less developed musculature: the stomachal epithelium consists of microvillar ciliated club-shaped cells; the caecal epithelium of microvillar vacuolar cells which have been observed under different metabolic stages (viz. they are flattened and without vacuoles or include either numerous small vacuoles or one very large vacuole); the intestinal epithelium of flattened microvillar cells. Digestive transit of alimentary particles has been studied through *in vivo* and histophysiological observations (using small coloured particles or ferritine as alimentary particles). When the myzostomid introvert is applied in an ambulacral groove, few alimentary particles are pumped and carried to the stomach by the contractions and the elongations of the pharyngial muscular fibers. In the stomach, they are chased out by means of ciliary beatings to the caeca where they are endocyted by caecal cells which are the site of intracellular digestion. After digestion, the alimentary residues included in large caecal vacuoles are exocyted by apocriny in the caecal lumen and are chased out to the stomach by the contractions of the caecal musculature. There, vacuoles and their residues are embedded in stomachal secretions to form a compact faecal mass which is expulsed through the anus by the contractions of the stomachal and intestinal musculature.

COST OF REPRODUCTION IN *OPHRYOTROCHA DIADEMA* (POLYCHAETA, DORVILLEI-DAE). *Eide, R. & Åkesson, B.* — (Department of Zoology, University of Göteborg, Box 25059, S-400 31 Göteborg, Sweden). — *Ophryotrocha diadema* is a simultaneous, cross-fertilising hermaphrodite. After pair formation each individual alternate in male and female function. Isolated individuals do not shed eggs. Reproductive costs were measured by comparison of life-tables obtained in four different experimental treatments. Reproduction, survival and growth (as number of setigerous segments) was recorded weekly during the whole lifetime of the animals. In older stages (> 20 weeks) a subjective "condition index" was estimated to evaluate sub lethal effects. For each experimental treatment 54 to 60 individuals were employed. The treatments were: 1. Continuous reproduction. Two individuals were permanently kept together with continuous possibility to reproduce. 2. Single. Individuals were isolated singly during their whole lifetime. 3. Half-time social. Reproducing pairs lived together for two weeks, they were then separated and each of them was placed together with an individual of *Ophryotrocha* sp., that is a sibling species. The two species have social interactions similar to intra specific ones, but inter specific mating does not occur. After two weeks with alien partners, the worms were placed with their conspecifics for the next two-week period of normal reproduction. Such two-week cycles continued during the animals' whole lifetime. This treatment was designed to lower physical reproductive effort but still maintain the social interaction. 4. Half-time single. This treatment resembles the one in n°3, but during the alternating two-week periods

Source : MNHN, Paris

with no reproduction the worms were kept singly isolated with no opportunity for social interactions. During peak reproduction (exp. weeks 7-8) the individuals with continuous reproduction had the best performance, followed by half-time single individuals. Lowest reproduction was found in the group of half-time social animals. All differences were significant. When the animals grew older the reproduction became similar in all three groups. During week 1-12 of the experimental period the fastest growth rate was found in the group of single individuals, followed in order by half-time single, half-time social and continuously reproducing individuals. All groups significantly differed from each other. At the end of the experiment, half-time single individuals were largest, while continuously reproducing and half-time social animals attained the same size. The lowest condition index was found in the group of single individuals during week 20-47. Half-time social animals had the highest condition index during week 20-25 but the lowest during week 47-52.

A FIRE WORM WITH A SHELTERED LIFE; STUDIES OF *BENTHOSCOLEX CUBANUS* (AMPHINOMIDAE), AN INTERNAL PARASITE OF THE BATHYAL SEA URCHIN *ARCHEOPNEUSTES HYSTRIX*. *Emson, R.H., Young, C.M. & Paterson, G.J.L.* — (Division of Life Sciences, King's College, University of London, Campden Hill Road, Kensington, London W8 7AH, U.K.). — *Benthoscolex cubanus* an amphinomid described by Hartman (1942), has been found in populations of the spatangoid sea-urchin *Archeopneustes hystrix* from bathyal depths (430-616 m) at several widely separated sites in the Bahamas area. The polychaete was found inhabiting the intestine of the sea-urchin where it feeds by selecting foraminiferans and other organic fragments from the gut of the sea-urchin. Twenty three species of sea-urchin were surveyed for the worm but *B. cubanus* appeared to be specifically associated with *A. hystrix*. The worm was abundant in that sea-urchin with an overall prevalence of 65 % and some populations were 100 % infected. Either one or rarely two worms were found in each urchin. The worm can move about easily in the gut of the sea-urchin but is not thought to leave the sea-urchin in normal circumstances. Mature worms were found in the populations at all times of year sampled and maturity was related to size. Sexes were equal and no difference in the size range of mature males and females was evident. *B. cubanus* was found to have small (80 µm) non-buoyant thick walled eggs and is likely to have a benthic or planktotrophic larva. Few obvious adaptations for life inside the gut of a sea-urchin were apparent but the structure of the cuticle was compatible with its having a protective function. *B. cubanus* is one of very few polychaetes living inside other animals and the only known internal parasitic polychaete of sea-urchins. Avoidance of predation appears to be the most likely reason for the evolution of this unusual relationship.

TAXONOMY AND POPULATION DYNAMICS OF *DIOPATRA CF. BREVICIRRIS* (POLYCHAETA, ONUPHIDAE) FROM THE MOROCCAN ATLANTIC COAST 1990-1992. *Fadlaoui, S., Lechapt, J.P. & Retière, C.* — (Laboratoire Maritime, 17 avenue George V, B.P. 28, 35801 Dinard, France). — *Diopatra* cf. *brevicirris* was collected near the south Moroccan Atlantic coast (North to South range: 31°58' to 31°52'; East to West range: 9°26' to 9°36'), at depths ranging from 16 to 40 m. *D.* cf. *brevicirris* is the dominant species in the benthic *Abra alba* community. This community is found in fine sediments which contain a varying degree of silt and are more or less compact. Thermal variations are not important because of the upwelling due to trade-winds. This species had not been reported from this coast until now, as it was probably confused with *Diopatra neapolitana*, a species from which it differs in certain characters. The structure and kinetics of this population were studied and the biological cycle of this species was described taking into account the climatic particularities of this area. Two sites were compared; site 1 was near the coast at a depth of 16 m, and site 2 was at a depth of 36 m. Partial weight of wiped subjects preserved in formalin was chosen as the biometrical criterion. Total weight was not used because the posterior part of individuals was frequently amputated during sampling and sifting, or following predatory attempts or autotomy. A frequency distribution histogram (N = 400) showed that most worms were broken at segment 10. Partial weight of the first ten segments was highly correlated with jaw lenght (r = 0.95). During the period of this study, spawning and recruitment periods were estimated from analysis of frequency distribution histograms; two periods of recruitment were identified in spring and summer 1990 due to consecutive winter and spring spawnings which take place in the tubes of adults and are followed by incubation and larval development unside these tubes. During summer 1991 we again observed recruitment, similar to that of the summer 1990. The reproduction cycle is certainly reproducible each year. Presence of some worms (partial weight < $5.10^{-3}$g) during winter and automn 1990 and observation of some worms, in July 1991, carrying eggs in tubes, suggest that order less important recruitments take place. In addition, as there were more young recruits at site 2 and adults were larger at site 1, we suggest that recruitment should take place at deep sites where the level of pelite is high.

CATALOGUE AND BIBLIOGRAPHY OF THE POLYCHAETES. *Fauchald, K. & Ward, L.A.* — (National Museum of Natural History, Smithsonian Institution, NHB Stop 163 Washington, D.C. USA). — Olga Hartman's publication of "Catalogue of the Polychaetous Annelids of the World" in 1959 (supplement published in 1965) was a major event for polychaete systematists and ecologists. The catalogue made it possible to look up the original description for almost all polychaete species published, when used in association with Hartman's previously published bibliography. References to combinations of genus and species names other than as originally published were also included. As at no time before, we had a single source of information of names at the species, genus and family-levels. The number of new taxa described in recent years has risen exponentially, in part due to the presence of the catalogue. Even the supplement is now close to 30 years old and a new edition is sorely needed. Computer applications for micro-computers are excellent for these kinds of publications. We have prepared a set of interlinked databases containing: 1. A listing of the original name for all

Source : MNHN, Paris

polychaete species; 2. References to new combinations of genus and species names, and 3. Complete bibliographic references to the polychaete literature from 1758 to date. This material will be issued as a compact disc. Printed copy can be prepared, or any data downloaded from any database on the disc. The disc will be a closed application: no more new material nor any additional queries for reports can be written to the disc. We will demonstrate the look and feel of the catalogue as currently devised. We would like the conference participants to spend time using the catalog, advise us about what kinds of documentation are needed and what uses to which they would put the catalog. We are at this point in the process of editing the content (probably a never-ending job!) but we are less concerned about having every last synonym entered, than we are about making the catalogue useful. Once we have a good format, we can continously edit the catalogue, taking into account new findings. We plan to issue periodic updates perhaps with 5 year intervals once the first version has become available. Polychaete systematics is an on-going task. We have been more concerned about having all current and recent points of view on a problem represented than about presenting a single, codified view of the systematics of any group. For this reason, we have been conservative in accepting proposed synonymies and have taken distinctly "agnostic" points of view in several conflicts.

PHYSIOLOGY OF OOGENESIS IN POLYCHAETES. *Fischer, A.* — (University of Mainz, Zoological Institute, Saarstr. 21, 6500 Mainz, Germany). — Oocytes generally are extremely large cells specialized for two purposes: storage of reserves and fusion with one male gamete. This review on physiology of oogenesis therefore gives account of the processes of growth and reserve accumulation in the oocyte and its differentiation as a gamete and, on the other hand, reports data on the physicochemical conditions the maternal soma is providing for the growing oocytes. In the period of vitellogenesis, the cytoplasm of the oocyte gets increasingly packed with storage inclusions containing yolk protein, lipid and carbohydrates, respectively. The cell membrane of the oocyte contains a receptor protein recognizing and internalizing yolk precursor protein at a specific rate. The various storage elements, more or less intermingled during vitellogenesis, are sorted out in a rapid process of egg maturation immediately prior to spawning in nereid eggs. Structural and biochemical differentiation of the vitelline envelope has been described in sabellids (Lee and coworkers). Which are the extracellular conditions required by growing polychaete oocytes? Environmental and hormonal parameters controlling oogenesis are known for a number of polychaetes, but physicochemical conditions immediately affecting the oocytes are defined in a few instances only. However, "diffuse" oogenesis without ovaries, common among polychaetes, offers favorable conditions for analyzing the immediate prerequisites for oocyte survival, growth and differentiation. Oocytes of *Nereis virens* can be kept in cell culture and their requirements, such as ionic composition, nutrient and oxygen contents of their medium can be defined. Likewise, oocyte physiology can be studied in the oocyte-nurse cell complex of *Ophryotrocha*. The specific conditions encountered in polychaete oogenesis thus may enable us to provide insights of general interest into the physiology of oogenesis.

CLADISTIC ANALYSIS OF RELATIONSHIPS AMONG THE POLYCHAETE FAMILIES. *Fitzhugh, J. & Fauchald, K.* — (Natural History Museum of Los Angeles County, Los Angeles, CA 90007, USA). — Some major taxa, e.g., the aphroditids and eunicids, both *sensu lato*, have been recognized consistently as natural groupings for 100 years. The traditional separation of the polychaetes into two groups and all other proposed groupings into suprafamilial taxa have been only moderately successful. Classsificatory studies differ from evolutionary studies in that the presence of links between the groups need not be specified. Most systematists believe that their classification, including the order in which the taxa are presented, reflect phylogeny. Any phylogeny based on these schemes would uncover paraphyletic groupings. We are here presenting a new phylogenetic analysis of the relationships among the polychaete families. We have analyzed the characters traditionally used to define taxa at the family-level and defined character states so that members of all families can be scored unequivocally. We have added, mostly anatomical, characters previously rarely considered, or at least considered only one at a time. We scored, if possible, the characters for a specimen of the type species of the type genus for each family (on classificatory rather than cladistic grounds): medium-sized to large specimens were used preferentially. Small specimens and indeed all specimens of small species, tend to have less developed anterior appendages, less complicated parapodia and often fewer kinds of chaetae than larger specimens (or species). We also assumed initially that all families as currently recognized were monophyletic. The cladistic program used was Hennig-86; options will be presented in the talk. Autapomorphic characters defining single terminal taxa were excluded from the analysis. We find it unlikely that for example the joint absence of the ventral shield of the sternaspids carry much weight as a synapomorphic feature for all non-sternaspid polychaetes. Outgroup taxa included echiurans and sipunculans in addition to oligochaetes. The major taxa listed above were confirmed as being monophyletic. The families of the Phyllodocida can be ranged together; similarly families with dorsal feeding palps (or some modification of these) can be grouped in a single sequence. We are at this point debating the position of other families, especially the orbiniids, paraonids, maldanids, capitellids, opheliids and the small families usually listed near these families.

POLYCHAETE POPULATIONS OF THE LEAF STRATUM OF A *POSIDONIA OCEANICA* BED: A YEAR CYCLE. *Gambi, M.C. & Lanera, P.* — (Laboratorio di Ecologia del Benthos, Stazione Zoologica "Anton Dohrn", Napoli, Italy). — In the framework of an investigation on vagile fauna of the Mediterranean seagrass *Posidonia oceanica*, Polychaetes were sampled in the leaf stratum of a continuous *Posidonia* meadow off Lacco Ameno (Island of Ischia, Gulf of Naples, Italy). Samples, taken by Scuba diving using a hand-towed net (400 µm mesh size), were collected monthly, from July 1981 to

Source : MNHN, Paris

June 1982, and along a transect, at 1 m, 3 m, 10 m, 15 m and 25 m depths. Monthly data, grouped in four seasons (summer, autumn, winter and spring) were analyzed by means of the Factorial Analysis of Correspondence. A total of 1,765 individuals and 134 species have been documented so far. Thirty seven taxa occurred only once with one individual, while 27 taxa (445 individuals) belonged to sessile forms and were not considered in this analysis. The best represented family was that of Syllidae (55 species and 865 individuals). A clear depth zonation of the populations was recognizable, especially in summer and spring when environmental differences between shallow and deep stands of the *Posidonia* bed are more pronounced. Seasonal differences were more evident at shallow depths (from 1 to 10 m), while these were almost negligible in deepest samples (25 m) where the environment is seasonally more stable. The most abundant species, best contributing to these spatio-temporal patterns were *Grubeosyllis clavata, G. limbata, G. vieitezi, Syllis prolifera, Platynereis dumerilii, Amphiglena mediterranea, Oriopsis armandi* and *Raphidrilus nemasoma* particularly abundant at shallow depth and in summer and spring, and *Sphaerosyllis pirifera, S. hystrix, Eurysyllis tuberculata, Odontosyllis gibba, Nereis rava* and *Kefersteinia cirrata* mostly occurring in deeper samples, especially in winter and autumn. As a whole, spatial and seasonal distribution of Polychaetes in the *Posidonia* leaf stratum was consistent with the environmental conditions of the bed and with the behaviour of other groups of the vagile fauna studied.

FEEDING ECOLOGY OF *PLATYNEREIS DUMERILII* (POLYCHAETA, NEREIDIDAE) IN *POSIDONIA OCEANICA* ECOSYSTEM. *Gambi, M.C., Zupo, V. & Mazzella, L.* — (Laboratorio di Ecologia del Benthos, Stazione Zoologica "Anton Dohrn", Napoli, Italy). — The Mediterranean seagrass *Posidonia oceanica* is characterized by a highly complex plant epiphytic community that shows successional stages culminating with a climax and a maximum of production in summer, especially at shallow depths. Most of this production is transferred to secondary producers by way of various species of grazers. *Platynereis dumerilii* is one of the most abundant Polychaetes in *Posidonia oceanica* meadows, representing almost 10 % of the total Polychaete abundance. This species is a hervivore mesograzer occurring in leaf stratum as well as in the rhizome layer of the plant, and it is particularly abundant at shallow stands of the beds (1-3 m depth) and in spring and summer. The feeding ecology of *P. dumerilii* was therefore studied to better define its trophic behaviour and its role in the food web of the *Posidonia* system. Specimens of *P. dumerilii* were collected in a shallow *Posidonia* bed of the Island of Ischia (Gulf of Naples, Italy) and in the surroundings hard bottoms, and reared in the laboratory (in a closed water system) for food-item choices and grazing experiments. All the experiments were conducted on starved animals divided in three size classes. Food choice experiments were conducted in binary chambers utilizing various species of macroalgae and *Posidonia* leaves differently epiphytized (without epiphytes, with encrusting corallinaceae algae and with erect algae). On the basis of the food choice results, forced grazing experiments were performed using plant-epiphytized *Posidonia* leaves. The fecal pellets produced were periodically removed and analyzed by means of optical and scanning electron microscopy. Grazed leaves were also examined for bite marks and other traces of grazing. Food choice experiments revealed that *Posidonia* with erect epiphytes was significantly preferred to the other items except for the brown alga *Dictyota dichotoma;* while *Posidonia* without epiphytes was heavely ever selected. This emphasises that epiphytic layer plays a greater role than the *Posidonia* tissues in the trophic ecology of this species, and it is consistent with the spatio-temporal distributional pattern of the species in such a system. Fecal pellet analysis showed the prevalence of macroalgae tissue in the diet of worms, regardless of their size class. However, fluorescence microscopy, revealed traces of undigested clorophyll in the fecal pellet material. *Posidonia* leaves grazed by larger worms (up to 15 mm length) showed clear grazing marks on erect macroalgae. These results help to better define the feeding behavior of *P. dumerilii* and demonstrate its potential role in the energy transfer at the *Posidonia* epiphyte level.

SOFT BOTTOM INTERTIDAL POLYCHAETES ASSEMBLAGES IN THREE ESTUARIES IN THE BASQUE COUNTRY (GULF OF BISCAY): TAXONOMIC STRUCTURES AND BIOCENOTIC AND ECOLOGICAL RELATIONSHIPS. *Garcia-Aberas, L. & Rallo, A.* — (Facultad de Ciencias, Zoologia, Universidad del Pais Vasco, Apdo, 644, 48080 Bilbao, Spain). — A general survey of polychaete fauna from littoral soft bottoms of three estuaries (La Arena, Plentzia y Mundaka-Basque Country, Spain) was done during the year 1989, and related to physicochemical conditions of the sediment and localisation of the sampling site. Over fifty species have been identified. Sample sites and the three estuaries as a whole have been characterised by faunistic richness, abundances, dominances and diversity indexes. Two main communities are present: the reduced *Macoma* in sites with mud (marshes) and the *Tellina* in sandy places. The accompanying species are investigated and discussed. A comparison has been made between the study areas based on the differing environmental gradients (granulometric data, organic enrichment, conductivity, temperature, pH, $0_2$ concentration and redox potential of the sediment) in order to determine the spatial distribution and temporal changes of polychaetes assemblages, and find out correlations between presence and abundance of species with those environmental conditions. It is concluded that granulometry and organic content are the most important factors determining the community structure.

CONTRIBUTION TO THE STUDY OF THE POLYCHAETOUS ANNELIDS FROM SOUTHERN IBERIAN PENINSULA: THE BAY OF ALGECIRAS (CADIZ, SPAIN). *Garcia-Martin, S. F.* — (Biologia, Facultad de Ciencias del Mar, Universidad de Cadiz, Apartado 40, 11510 Puerto Real, Cadiz, Spain). — The bay of Algeciras (Cadiz, Southern Spain) spreads over 70 $km^2$, with maximum depths of 500 m. During last decades it has undergone both considerable industrialization and human

Source : MNHN, Paris

population increase. Several harbour constructions in this bay cause decreased water renewal rates in some areas. However, the bay of Algeciras is located in a region with a strong hydrodynamic regimen (Strait of Gibraltar); this location counteracts the effects of sewage and industrial waste discharges. This preliminary report presents a checklist of Polychaetous Annelids (about 100 species) from several areas of the bay of Algeciras (depths of 0 to 27 m). The data obtained are discussed in relation to human activities and type of bottoms, and compared with others from adjacent areas which are pressumably unpolluted.

*NOTOMASTUS LATERICEUS* VS *NAINERIS LAEVIGATA*, TWO CONFLICTING STRATEGIES COMPETING IN THE SAME HABITAT. *GIANGRANDE, A. & PETRAROLI, A.* — (Dipartimento di Biologia, Università di Lecce, 73100 Lecce, Italy). — A study over three years in the Acquatina lagoon (South Adriatic Sea, Italy) was carried out to investigate the reproductive strategies of several polychaete species. The life-history traits of dominant species, *Naineris laevigata* Grube and *Notomastus latericeus* Sars, showing contrasting reproductive strategies, were compared. The first species is a polytelic long lived form characterized by a slow growth rate and high juvenile mortality. *N. latericeus is* a monotelic annual species characterized by fast growth and high adult mortality. The *N. laevigata* reproductive cycle seems to correspond to a bet-edging strategy with a storage effect, which allows this species to respond to a fluctuating environment, and to maintain stable trends of abundance and biomass. By contrast the survival pattern of *N. latericeus*, showing a rapid increase in favourable periods, could be classified within the opportunistic scheme of large recruitment over a very short period of time followed by high adult mortality. This leads to very variable trends in abundance and biomass of this species. The abundance of *N. latericeus* in the lagoon is mainly the result of successful recruitment strongly related to the variation in salinity and competition with other polychaete species. During most of the time, in which the salinity ranged from 20 to 30 P.S.U. *N. laevigata* seems to be competitive superior and *N. latericeus* remains confined in well defined patches. Some evolutionary problem arising from the reproductive strategy of *N. latericeus* are also discussed.

DISTRIBUTION OF ONUPHID POLYCHAETA IN THE NORTH ATLANTIC, FROM TROPICAL TO ARCTIC PROVINCE. *GLÉMAREC, M., INTÈS, A. & POCKLINGTON, P.* — (Université de Bretagne Occidentale, 6 Avenue le Gorgeu, 29287 Brest Cedex, France). — The taxonomy of Onuphid family has been well reviewed by a number of authors, allowing to define the different ways of colonization in the whole North Atlantic Ocean. Bathymetric and latitudinal distributions are the main sources of informations helping to recognize biogeographic contingents. A previous study for the Northeast Atlantic showed high diversity of the bathyal slope, compared to the shelf area. Stable conditions provided shelter to the marine fauna, after the "Pliocène-Pleistocène" variations of sea level. From this stable area, abyssal plains might have been colonized since the recolonization of the shelf appeared when the glaciers declined. The authors propose to transfer these concepts to the Northwest Atlantic. In this geographic area, actual and quaternary hydroclimatic conditions should be different. The distribution of Onuphids in the eastern Tropical Atlantic was studied according to the same principles (bathymetry and latitude), especially on the continental shelf of Ivory Coast. Climatic regions (étages) can be compared to the european system. The horizontal distribution shows faunal cuts in relation with the seasonal settling of the frontal zones. Submergence of temperate species in these tropical latitudes, emergence of some other contingents and relative scarcity of tropical species, can be explained by the regional hydroclimatic characteristics. Relations with the eastern South Atlantic on one hand, and with the Caribbean region on the other hand, can be inferred. Amphi-atlantic distribution of Onuphids in arctic, temperate and tropical provinces can be also estimated for the shelf, bathyal and abyssal zones.

A COMPARISON OF SPECIES DIVERSITIES OF POLYCHAETES FROM TEMPERATE AND TROPICAL LOCALITIES. *GOBIN, J.F.* — (Plymouth Marine Laboratory, West Hoe, Plymouth PL1 3DH, U.K). — Artificial substrate units (nylon pan scourers) were deployed on rocky bottom substrates in the South West of England (UK) and in Trinidad and Tobago (TT), West Indies. Units were left submerged for similar durations of time (April-October 1990 in the UK and January-July 1991 in TT). Some units were retrieved at fixed intervals (colonisation experiment) and all others were retrieved after the 5 month period (final diversity). 1,817 individuals representing 73 species were identified for UK and 1,842 individuals of 93 species were counted for TT. Diversity indices (SWI) for UK samples ranged between 0.75 and 2.5 and for TT between 1.7 and 2.45. Species of the family Syllidae were the initial colonists and also the most dominant family in both areas. Initial colonisation was much faster in TT but the final polychaete diversities were similar for both localities. For both sets of samples, species were aggregated into families and showed similar development of "parallel communities" (THORSON, 1957). Results appear to be contradictory to the latitudinal gradient in species richness theory.

UNUSUAL FATE OF PCBS IN *HEDISTE (NEREIS) DIVERSICOLOR* (POLYCHAETA, NEREIDAE). *GOERKE, H. & WEBER, K.* — (Alfred-Wegener-Institut fur Polar-und Meeresforschung, Am Handelshafen 12, Postfach 120161, D-2850 Bremerhaven, Germany). — The elimination kinetics of six polychlorinated biphenyl components were investigated in *Hediste diversicolor* and for comparison also in *Platichthys flesus*. Animals from the Weser estuary were maintained at 10 °C and 10 P.S.U. in water continuously filtered through charcoal and given 10 oral doses of a mixture of the PCB components 52, 44, 95, 101, 87, 153 (IUPAC Nos.; total dose per component: 1 $\mu g.g^{-1}$ wet wt.). At regular intervals during the subsequent elimination period, specimens were analyzed for the six components. The observed PCB

Source : MNHN, Paris

concentrations in the animals enabled elimination half-lives to be determined. Ragworms eliminated all components, except Nos. 95 and 153, faster than flounders. The slow elimination of No. 95 in ragworms is remarkable, because this component has unsubstituted carbon atoms in 3.4 position, which generally facilitates biotransformation. These results indicate specific PCB elimination pathways in *H. diversicolor* rather than a generally enhanced elimination rate. The analysis of the fate of component 52, which had been $^{14}C$-labelled, revealed that its faster elimination was due to significant biotransformation: *H. diversicolor* contained considerably more polar transformation products than *P. flesus*. *H. diversicolor* from the upper, more contaminated Weser estuary also formed more $^{14}C$-labelled polar compounds than those from the lower estuary. Since different salinities did not influence the PCB elimination, the elevated biotransformation capacity of *H. diversicolor* from the upper estuary is explained by enzymatic induction. The patterns of PCB elimination half-lives in *H. diversicolor* and *P. flesus* were in accordance with the PCB concentration patterns determined in environmental samples of the species. While PCBs in *P. flesus* were similiar to Clophen A60 presumably prevailing in the field, this was not true in *H. diversicolor*. Therefore, it is concluded that species-pecific PCB elimination influences the PCB concentration pattern in *H. diversicolor* significantly.

POLYCHAETE LARVAL SETTLEMENT DYNAMICS IN THE BAY OF BANYULS, NW. MEDITERRANEAN. *Grehan, A.J.* — (Observatoire Océanologique de Banyuls, Laboratoire Arago, 66650 Banyuls-sur-mer, France). — This study was undertaken to highlight the major differences in benthic invertebrate settlement patterns at two sites in the Bay of Banyuls, NW Mediterranean. The sites, although in close proximity spatially, are characterised respectively as belonging to a fine sand *Spisula subtruncata* community (20 m) and a muddy sand *Nephtys hombergii* community (30 m). Intensive weekly diver sampling of the superficial sediment (0-2 cm) at both sites was undertaken during the main spring settlement period (March-July). Samples were sieved at 100 µm to ensure complete census of settlers. The results of this study, for the Polychaeta, are reported and discussed in the light of measured environmental parameters.

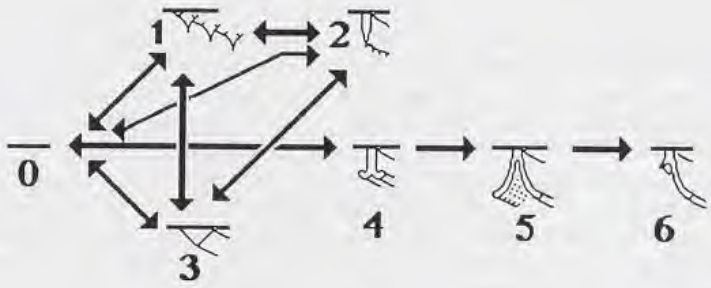
SPECIES RECOGNITION AND REPRODUCTIVE ISOLATION IN NEREIDS (ANNELIDA POLYCHAETA). *Hardege, J.D., Bartels-Hardege, H. & Zeeck, E.* — (University of Oldenburg, Inst. Chem. Biol. Mar. Environm., C.v. Ossietzky Str., W-2900 Oldenburg, Germany). — The reproductive form of *Nereis succinea* and *Platynereis dumerilii* is the metamorphosed heteronereis, which is highly specialized for reproduction, has a distinctive reproduction behaviour the swarming and nuptial dance and die after fertilization. The induction of metamorphosis to ripe heteronereids and the determination of date of swarming are controlled by endogenous rhythms, temperature regimes and moon light ("zeitgeber"). In the Danish Isefjord *P. dumerilii* reproduces in summer at 3 rd. quarter of the moon cycle while *N. succinea* swarms around the new moon phase. However there is an overlap of swarming activity of these species during the week after new moon phase due to weather conditions. The sex pheromone of *P. dumerilii*, 5-methyl-3-heptanone was likewise found in *N. succinea* where it is also active. The pheromone induces an increase in swarming activity during the nuptial dance behaviour, allows sex recognition by use of sex specific enantiomers and the release of a small cloud of sperm in males. In *N. succinea* the threshold concentration of the pheromone is 25 times higher than in *P. dumerilii*. Here species recognition and reproductive isolation is provided by the sex pheromone which prevents direct contact of the two species.

HIGH POLYCHAETE DIVERSITY IN THE DEEP SEA: PATTERNS OF α AND ß, DIVERSITY. *Hilbig, B. & Blake, J.A.* — (Science Applications International Corporation, 89 Water Street, Woods Hole, Massachusetts 02543, U.S.A). — Diversity may be described as the number of species in a spatially defined point (α-diversity) or the turnover of species across a gradient (ß-diversity). Data on species diversity is typically described in terms of local or α-diversity in a restricted spatial setting. We know little about the restriction of individual species, especially in the deep sea where there are few barriers to long distance distributions. One difficulty in assessing the distributions of deep-sea polychaetes has been the lack of appropriate samples and the lack of opportunities for single investigators to examine samples from widely separated geographic locations. We have been able to identify polychaetes from continental slope depths on both the western North Atlantic and eastern Pacific from similar depths (550-3,000 m). Samples from the western North Atlantic included 550 quantitative box cores taken from the Canadian boundary to off South Carolina. Samples from the eastern Pacific were focused in the Gulf of the Farallones off San Francisco and included 67 quantitative box cores. Some additional material from ambient sediments on the Gorda Ridge in 3,000 m off Oregon were also examined. All samples were sieved through 300 µm screens and subsequently processed in the same manner. We found a total of 708 polychaete species on the U.S. Atlantic slope and at least 250 species in the eastern Pacific. The number of Pacific species is preliminary because investigations on this material are still on-going. We expect the number of Pacific deep-sea species to increase. Of the Atlantic species, 315 were widely distributed throughout the entire study area, while 92 species were restricted to the slope off New England, 42 species were found only off Delaware and New Jersey, and 177 species were restricted to the slope off the Carolinas. About 50 species were shared between the Atlantic and Pacific slopes. It seems therefore that we can distinguish between several distributional patterns of deep-sea polychaetes: local (restricted to a small area, found at only one or a few stations in either the Atlantic or the Pacific), regional (present at many stations on either the Atlantic or the Pacific slope), and global (present in both the Atlantic and Pacific oceans, often along depth contours). The largest group of polychaetes with global distribution was the Dorvilleidae with 10 species belonging to eight genera; other families including a fairly large number of globally distributed species were the Paraonidae (six

Source : MNHN, Paris

species, four genera), Ampharetidae (five species, five genera), and Spionidae (five species, three genera). Additional families, represented by one or two species, were Apistobranchidae, Cirratulidae, Fauveliopsidae, Glyceridae, Hesionidae, Nereididae, Onuphidae, Opheliidae, Paralacydoniidae, Pholoidae, Phyllodocidae, Pilargiidae, Scalibregmatidae, Syllidae, and Trichobranchidae.

A CLADISTIC ANALYSIS OF *SPIRASERPULA* REGENHARDT, 1961 (SERPULIDAE, POLYCHAETA); CHARACTERS AND CHARACTER STATES. *Hove, H.A., Ten & Pillai, T.G.* — (Instituut voor Taxonomische Zoologie, P.O. Box 4766, 1009 AT Amsterdam, Netherland). — In the course of a revision of the genus *Serpula* (Pillai, in prep.), a unique and in serpulids hitherto unknown set of intemal tube structures (i.t.s.) was discovered in a yet undescribed species from the Cape Verde Islands and Florida. The hunt in our collections for more tubes with these longitudinal intemal ridges of startling complexity resulted in another 15 new species, from various (sub)tropical localities. Some are scissiparious, a so far for the genus *Serpula* unknown reproductive method. Though overlooked in the descriptions of *S. lineatuba, S. massiliensis* and *S. minuta*, these taxa too showed i.t.s. Finally i.t.s. were found in the type-species of *Spiraserpula, S. spiraserpula*, erected by Regenhardt (1961) for Cretaceous-Paleocene species. The recent species can be included in this genus, apparently of Tethyan origin. Delimited by a clear-cut synapomorphy, presence of i.t.s., it is monophyletic. The additional character set of intemal tube structures (and a fossil record) makes the genus *Spiraserpula* more suitable for phylogenetic analysis than other serpulid genera without i.t.s. By its setal complement and *Serpula*-type operculum (if present), *Spiraserpula* evidently is a member of the *Serpula/ Crucigera/ Hydroides* clade. As outgroup we have selected *Serpula oshimae* and *S. rubens*. Evidence from various transformation series was conflicting, and a manual construction of a phylogenetic tree was out of the question. We had to recourse to the following programs for PC's: HENNIG 86 (for MsDOS machines), Paup & MacClade (for Macintoshes). Characters used are numerical, meristic and/or morphological; states may vary from simple yes/no to complicated hypotheses of transformation series, with up to 10 states. They included tube, operculum, branchiae, thorax, setae and uncini. Each type of character presents its peculiarities: in morphological data questions of homology and polymorphy have to be solved; although numerical and meristic data are discrete, delimiting size classes poses problems. Some of these problems may be exemplified by the character "internal dorsal ridge". Its states are: none = 0; loose teeth =1; toothed ridge = 2; smooth triangular = 3; smooth plate with thickened edge, T = 4; Y (inverted, stalked V) = 5; askew = 6. The sequence of character states 4-5 is found along a single ridge in two species. There are two reasons to assume that the character evolved from state 5 to 6 and not the other way around: 1) bilateral symmetry is the plesiomorphous condition in Sabellida, 2) asymmetry might be a functional response to a curved tube (although in spirorbids it rather appears to be the other way around). A possible transformation series is given below. It is neither known if there has been a direct step 1-3 or 0-2, nor if the sequence has been 0-1-2 or rather 0-2-1. Thus states 0-3 should be treated as unordered, but the assumption ordered (irreversibly) might apply to states 4-5-6. In computer analysis, "unordered" may be best for the entire set of states, even though this probably implies some loss of information. In the course of the analysis, the choice of characters was narrowed down. The final matrix, consisted of 20 species (including outgroup) and 22 characters. HENNIG 86 option mhennig*, bb* results in 1 cladogram (l = 148, ci = 41, ri = 57). The relatively low consistency index indicates that it still should be regarded as a preliminary hypothesis.




HABITAT SELECTION BY SETTLING LARVAE OF THE SPIONID *PSEUDOPOLYDORA DIOPATRAE*. *Hsieh, H.L.* — (Institute of Zoology, Academia Sinica, Taipei, Taiwan 11529, Republic of China). — The natural populations of the spionid *Pseudopolydora diopatrae* predominantly inhabit the tube-caps of the onuphid *Diopatra bilobata* and rarely found in bare sand areas. Habitat selection by competent larvae of *P. diopatrae* was studied in the laboratory from December 1990 to August 1991. The relative importance of chemical and physical characteristics of tube-caps to larval settlement was examined. Experimental results showed that the spionid larvae made choices among the habitat types provided. Larvae significantly preferred the tube-caps rather than bare sand, a pattern consistent with the spatial distribution of

Source : MNHN, Paris

their natural populations. When the tube-caps were disassembled, the larvae no longer chose to settle in the remains, regardless of retained chemical characteristics. The larvae seemed to respond to physical setting of the habitat rather than chemical one. The physical setting of the tube-caps was characterized as stable, firm and structural. The larvae that settled on the tube-caps within 10 days were larger than those on other habitat types, implying that there is selective advantage for those individuals choosing tube-caps as settling sites.

MORPHOLOGICAL INVESTIGATIONS ON SOME POLYCHAETE LARVAE OF THE PLANKTON AROUND HELGOLAND (GERMAN BIGHT). *HUSEMANN, E. & PLATE S.* — (AG Entwicklungsphys. d. Tiere, Lehrstuhl f. Spez. Zool. & Parasitol., Ruhr-Universitat Bochum, Postfach 10 21 48, D-W4630 Bochum 1, Germany). — During a three year plankton monitoring in the German Bight near Helgoland, pelagic larvae of 57 benthic polychaete species were found. Literature descriptions of developmental stages are missing or incomplete for 15 of the observed species. Here the discriptions of some so far unknown larval stages of four species are given. The earliest planktonic stages of all four species are eggs and trochophores, respectively. Pelagic trochophores of *Scoloplos armiger* (Orbiniidae) are ovoid and possess a strong ciliation. At the beginning of segmentation one pair of red eyes becomes visible. The metatroch segment and three presumptive setigers are differentiated first. At settlement larvae possess 11 segments, all bearing chaetae except the metatroch segment. A pair of gills becomes visible at the 10 th setiger. The ciliation which is present in all segments is reduced up to settlement from anterior to posterior. Uncleaved eggs are the earliest pelagic stage of *Scolelepis bonnieri* (Spionidae). They are ovoid and characterized by a thick, sculptured egg membrane. The egg membrane is first penetrated by the prototroch cilia which serve for active movement and later by the larval chaetae of the developing embryo. In the 3-segment stage the egg membrane fuses with the larval cuticle. The prostomium of older larvae becomes trapezoid and possesses two pairs of red eyes and a retractile tip. Larvae with 10 segments have a length of 650 µm. Olive-brown pigmented trochophores with a mean length of 300 µm are the earliest planktonic larval stage of *Eulalia viridis* (Phyllodocidae). They possess a well developed prototroch and one pair of eyes. The prostomium of the metatrochophores is blunt conical and 4 antennae buds become visible. In this stage 6-7 segments are developed. Tentacular cirri originate in the 1st and 2nd segment, ventral cirri occur from the 3rd and dorsal cirri from the 4th segment onward. Composed chaetae are present from the 2nd segment onward. The average length of early nectochaeta with eight segments is 500 µm. The prostomium is now trapezoid, longer than wide, and anterior, in front of the eyes, a 5th median antenna becomes visible. The 4th pair of tentacular cirri appears in the 17-19 setiger stage. The opaque trochophores of *Pholoe minuta* (Sigalionidae) are 150-200 µm long and possess a well developed prototroch. Metatrochophores with five segments have a mean length of 450 µm. Their only differentiation at the prostomium are two pairs of eyes, while the trunk segments are well developed and bear parapodia with chaetae. Elytrophores with papillae are present in the 2nd, 4th and 5th segment, a small conical dorsal cirrus in the 3rd segment. The development of elytra starts before the prototroch is reduced completely, so the latest pelagic stages possess small round elytra.

TOWARDS GENERIC REVISION OF AMPHARETIDAE. *JIRKOV, I. A.* — (Hydrobiology Department, Biological Faculty, Moscow State University, Moscow, 119899, Russia). — Seventy seven considered as valid ampharetids genera include only 200 valid species. It means one ampharetids genus consist of only about three species or three time less than other polychaete genus do. Forty seven genera are monotypic the highest amount within Polychaeta. An investigation of individual variation of external morphological (including structure of setae) features, using or proposed for using as taxonomical ones on specific or generic level shows that some features are distinctly length-related, such features can be used even at specific level carefully. Other features are not length-related, among them are features of specific, generic or higher levels. Some features are age-related and variation of them in adults reflects preservation of juvenile conditions. And minimum one feature is length-related in some genera and is not length-related in other ones. An investigation of rules of interspecific variation of a feature, an estimate of relation and correlation between features, leads not only to more precisely specific description, but also at present time allows to determine the taxonomical value (to do feature weighting) almost of all external morphological features. One of the basis idea of this estimate is: if a variation of a feature is *intraspecific* this feature cannot be used for *generic* classification. Despite the idea is obvious, it immediately crashes modern system. It is offered to base generic classification on following characters: within Ampharetinae a type of prostomium and a type of modification of thoracal segments, amount of branchiae; within Melinninae presence/absence of dorsal hooks and crest. Such features as amount of thoracal setigers and uncinigers, branchial structure, all features of abdomen and above this within Ampharetinae degree of the paleae developing, and within Melinninae amount of the branchiae, presence of buccal tentacles of different size and amount of dorsal crests and hooks should not be used for this porpoise. As a result near 1/3 of the whole number of ampharetids genera (at least 25) have to be turn to junior synonyms. Some features allow to group genera and make conclusions about the most possible ways of evolution within ampharetids and theirs relations with other Terebellomorpha and group Ampharetinae in four tribes.

THE ULTRASTRUCTURE OF A GUTLESS ANNELID, *PARENTERODRILUS* G. N. *TAENIOIDES* (= *ASTOMUS TAENIOIDES*)(POLYCHAETA, PROTODRILIDAE). *JOUIN-TOULMOND, C.* — (Université Paris VI, 4 Place Jussieu, 75252 Paris Cedex 05 et Station Biologique CNRS-UPR 4601, 29680 Roscoff Cedex, France). — An ultrastructural investigation of the mouthless protodrilid *Parenterodrilus taenioides* (JOUIN, 1979) shows that the residual gut, with its very narrow, ciliated lumen has lost any digestive function. Salivary glands are retained in some anterior segments and

Source : MNHN, Paris

their canals converge in a ventral area of the prostomium and open at the epidermal surface. The epidermal ciliation is much more developed than in any other protodrilid species. In the middle and posterior body segments, the enlarged epidermal surface area is covered by a cuticle bearing an array of epidermal microvilli which probably are the site of active transport of dissolved organic compounds. The presence of numerous subcuticular coated vesicles and lysosomes in the support cells suggests that particulate material from the ambient milieu is taken up by endocytosis and finally digested in the epidermis. The origin and nature of the organic substances that constitute the food of *P. taenioides* are still unknown. Experiments have been made on living animals with ferritin added directly to the seawater and left in contact with the animals for different times. After a contact of 30 min with ferritin, the epidermis of *P. taenioides* has few subcuticular coated vesicles containing ferritin, this substance being already concentrated in endosomes in the apical part of the epidermal cells and in secondary lysosomes, more basally. There are no symbiotic bacteria in the cuticle, epidermis or residual gut of *P. taenioides*. Abundant intracellular crystals in the nonfunctional gut indicate that this residual organ plays a role in the bioaccumulation of environmental substances which enter the body through the epidermis. The epidermis is the only absorptive surface of this unique polychaete devoid of both a functional gut and symbiotic bacteria.

POLYCHAETES OF THE RIA DE FOZ (GALICIA, SPAIN). *Junoy, J. & Viéitez, J. M.* — (Departamento de Biologia Animal, Universidad de Alcala de Henares, E-28871 Alcala de Henares, Madrid, Spain). — Polychaete macrofaunal (> 1 mm) species distribution and community structure of an intertidal soft-bottom estuary, the Ria de Foz (Galicia, northwest Spain) was investigated during the years 1984, 1985 and 1986. The sampling programme consisted in two sampling periods. First period (December 1984 to March 1985) was adjusted to provide adequate information of polychaete species and consisted of 99 samples widely distributed along the estuary. These samples yielded 9,419 individuals belonging to 40 polychaete species. *Manayunkia aestuarina, Alkmaria romijni* and *Ophelia rathkei* were firstly recorded for the Spanish waters. The analysis indicated that sediment characteristics and tidal height were the most important factors governing the distribution and abundance of polychaete species. On the second sampling period (June 1985 to April 1986) eight stations were visited at six occasions to know the fluctuations of the most abundant polychaete species (e. g., *Pygospio elegans, Spio martinensis, Capitella capitata, Heteromastus filiformis, Hediste diversicolor*). A total of 38,659 individuals of 38 polychaete species were collected at these 48 samples.

THE EXPERT SYSTEM "NEREIS" FOR POLYCHAETOUS ANNELIDS FROM FRANCE. *Jussien, N., Verger, V., Gillet, P. & L'Hospitalier, Y.* — (Université Catholique de l'Ouest, 3 place André Leroy, BP 808, 49008 Angers Cedex 01, France). — In his Faune de France volume on the errantiate polychaetous annelids, Fauvel (1923) listed only 15 families (not counting the parasitic Histriobdellidae and Ichthyotomidae). There are presently 30 families found along the coast of France and it was therefore necessary to revise the key to the families for a computerised systematics software program. The program "Nereis" was developed by "Syspertec" using the language "Xi Plus".

THE TAXONOMY AND COMPARATIVE MORPHOLOGY OF THE GENERA IN THE FAMILY SABELLARIIDAE JOHNSTON, 1865 (ANNELIDA, POLYCHAETA). *Kirtley, D.W.* — (Florida Oceanographic Society, Hutchinson Island Coastal Science Center, 890 N.E. Ocean Boulevard, Stuart, Florida 34996, U.S.A.). — An extensive reexamination of accessible specimens in repositories, personal field collections, and material received through loans and donations coupled with a critical review of accessible taxonomic accounts in the literature (Kirtley, in press) discloses the presence of certain well defined morphological characteristics within the various genus- and species-groups in the family Sabellariidae. These anatomical variations can be applied as criteria for the organization of the known taxa into two subfamilies and some 11 genera. The subfamily Sabellariinae comprehends all the sabellariid genus-groups 3 parathoracic segments. The subfamily Lygdaminae includes all the known genera of Sabellariidae having four parathoracic segments (Kirtley, in press). This proposed ordering is consonant with the observations of Caullery (1913) who enunciated the same principle in proposing two genus-group names: *Pallasia, sensu stricto* for those species with three parathoracic segments and *Tetreres* for those species with four. Subsequent authors, notably Johansson (1927) and Hartman (1944) found Caullery's usage essentially inappropriate and grouped the known species into the seven genera recognized at that time. Both authors included the genus *Cryptopomatus* Gravier, 1908. This name is now considered to be an invalid synonym of *Idanthyrsus* Kinberg, 1867 (Kirtley, in press). The previously recognized six genera, namely: *Sabellaria* Lamarck, 1812; *Phragmatopoma* Morch, 1863; *Idanthyrsus* Kinberg,1867; *Lygdams* Kinberg, 1867; *Phalacrostemma* Marenzler, *Gunnarea* Johansson, 1927 are complemented by an additional four genera which have been defined and included in the family. Lechapt & Gruet (1993) have recenty described yet another previously unknown genus-group from off New Caledonia in the southwest Pacific Ocean; bringing the number of presendy recognizable genera to 11. The criteria invoked to systematize the nomenclature of the genus groups and the specific characteristics that define and identify the many species within these genera are outlined and discussed.

THE ORDER AMPHINOMIDA: A REVISION OF THE FAMILIES (ANNELIDA, POLY-CHAETA). *Kudenov, J.D.* — (Department of Biological Sciences, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, Alaska 99508 U.S.A.). — The order Amphinomida (Annelida) *sensu* Fauchald (1977) is monotypic (Fauchald, 1974), and strongly isolated in the class Polychaeta. No other living order or family approaches the Amphinomida. Although this order is

Source : MNHN, Paris

well recognized within the class, the assignation of families within can be rather controversial. The basis of this continuing argument centers on the nature of one's understanding about this group and personal philosophy (KUDENOV, 1991, 1992). Workers today recognize one of two classification systems. (1) a single family (Amphinomidae) representing three subfamilies (Amphinominae, Euphrosininae, Archinominae); or (2) three separate families without subfamilies. Irrespective of which classification is preferred, the order contains at least one paraphyletic family; its resolution into monophyletic taxa produces a revised family classification and redistribution of existing genera. The purpose of this study is to present preliminary results of cladistic analyses based on detailed morphological examinations of species for 18 of 24 described genera in the order Amphinomida. Type materials were examined whenever possible. It was sometimes necessary to examine specimens of well known species since those of the type genus were not readily available. The following genera were examined: *Amphinome rostrata* (Pallas, 1766); *Archinome rosacea* (Blake, 1985); *Benthoscolex microcarunculata* (Treadwell, 1901); *Branchamphinome antarctica* Hartman, 1967; *Chloeia flava* (Pallas, 1766); *Euphrosine myrtosa* Lamarck, 1818; *Euphrosinella cirratoformis* (Averincev, 1972); *Euphrosinopsis antipoda* Kudenov, 1992; *Eurythoe complanata* (Pallas, 1766); *Hermodice carunculata* (Pallas, 1766); *Hipponoa gaudichaudi* Audouin & M. Edwards, 1833; *Notopygos crinita* Grube, 1855; *Paramphinome pulchella* Sars, 1872; *Pareurythoe japonica* Gustafson, 1930; *Pherecardia lobata* Horst, 1886; and *Pseudeurythoe paucibranchiata* Fauvel, 1932. Species not included in this study generally reflect the unavailability of specimens; these are discussed. In all, 72 characters including 173 binary and multistate characters-suites were analysed using HENNIG 86. The analysis is unpolarized since a suitable outgroup does not seem to exist. A cladogram having minimum tree lengths is presented for the order; CI and RI values are also reported. Separate groups are recognized and discussed. Transformation series are presented for each family and genus. Phylogenetic relationships between families and genera are also discussed, particularly in regards to ideas advanced by GUSTAFSON (1930).

POPULATION DYNAMIC OF POLYCHAETES IN THE SUBTIDAL SOFT BOTTOMS IN THE BAY OF SANTANDER (NORTH OF SPAIN). *LASTRA, M., SANCHEZ, A., PALACIO, J. .& MORA, J.* — (Departamento de Biologia Animal, Universidad de Santiago de Compostela, 15706 Santiago de Compostela, La Coruña, España). — Polychaetes are the dominant taxa in the softbottoms of the subtidal environments in the Bay of Santander. Its seasonal dynamics takes on an differential behavior in various environments analized. The inner areas of the bay are occupied by faunistically rich communities, where *Melinna palmata, Spiochaetopterus costarum* and *Chaetozone setosa* are the main species. The presence of this tube dwelers Polychaetes (*M. palmata* and *S. costarum*) can promote the settling process of many species (YOUNG & RHOADS, 1971). In the terminal inner areas of the bay, the Polychaetes community, settled on clayish sediments, is similar to the rest of the inner areas but with an evident qualitative and quantitative reduction. In the areas affected by harbor dredging activities, *C. setosa, Notomastus latericeus, Polycirrus pallidus* and *Mediomastus fragilis*, are the more abundant species, and its density hardly increase when the dredging activities disappear. In the areas affected by urban sewage, the community is dominated by subsurface deposit feeders, specially *N. latericeus* and *Euclymene oerstedii*, whose densities ranged between 50 and 300 ind. $m^{-2}$ and make up 60 % of the total density of the community. In the oceanic influenced area, faunistically dominated by small Crustaceans (amphipods and pagurids), *Nephthys cirrosa* is the only Polychaete present during all year, making up the 10 % of the total density in the community, and the 5 % of its biomass.

BATHYAL AND ABYSSAL SABELLARIIDAE (ANNELIDA POLYCHAETA) FROM NEAR NEW CALEDONIA (PACIFIC OCEAN). *LECHAPT, J.P. & KIRTLEY, D.W.* — (Laboratoire maritime de Dinard, MNHN, 17 av. George V, 35800 Dinard Cedex, France). — Except for the relatively limited accounts of HOAGLAND (1920), TREADWELL (1926), CAULLERY (1944) from the Philippines and Indonesia, and that of GIBBS (1971) from the Solomon Islands, the benthic polychaete fauna from great depths of this geographic area remains poorly known. New information has been provided by study of benthic collections made during several French cruises conducted in recent years near New Caledonia. Specimens described in this work were collected during the BIOCAL and BIOGEOCAL cruises in 1985, which were organized by the Muséum National d'Histoire Naturelle. The material was received from the "Centre National de Tri" (Brest, France). All of the 488 specimens in the collection, collected from depths between 440 and 1,870 m, belong in the subfamily Lygdaminae defined by KIRTLEY (in press). This group is characterized by the presence of four parathoracic segments. Among these specimens we are able to identify a total of four genera, including the newly described genus *Bathysabellaria* Lechapt & Gruet, 1993, and six species which are thought to be new to science. The collection includes a new species in the genus *Lygdamis* Kinberg, 1867; two new species in the genus *Phalacrostemma* Marenzeller, 1895; a new species in the genus *Tetreres* Caullery, 1913; and two new species in the new genus *Bathysabellaria*. Sabellariids, like most benthic organisms, appear to be uniquely adapted and constrained to relatively restricted biogeographic and depth domains. In the sabellariid groups apparently restricted to the near shore "surf" zone this stenotopic habit is emphatically demonstrated.

*NEREIS RIISEI* GRUBE 1857 (POLYCHAETA, NEREIDIDAE): RELATIONSHIP BETWEEN BODY LENGTH, SPECIES SPECIFIC CHARACTERS, AND REPRODUCTIVE STATE. *LONG, C.D.& SCHOENER, A.* — (The Buffum Group, 21 1/2 Buffum Street, Salem, MA 01970, U.S.A.). — Specimens of *Nereis riisei* Grube, 1857 (limited to the Caribbean and associated waters) from museums in Europe and the United States were studied for relationship between body length and

Source : MNHN, Paris

(1) number of paragnaths (by area), (2) appearance of the first notopodial falciger in asexuals, (3) reproductive state, and (4) development of sexual products.

SOFT BOTTOM POLYCHAETES FROM THE WESTERN COAST OF BAJA CALIFORNIA SUR, MEXICO: ONUPHIDAE. *LEON-GONZALEZ, J.A. DE.* — (Laboratorio de Zoologia de Invertebrados, Facultad de Ciencias Biologicas, Universidad Autonoma de Nuevo Leon, Apartado Postal 5, Suc. "F", San Nicolas de los Garza, Nuevo Leon, 66451 Mexico). — Eleven species and four genera of Onuphidae have been identified from the soft bottom environment along to the western coast of Baja California Sur, Mexico, in the continental shelf at 40 to 220 m depth: *Diopatra farallonensis* Fauchald, 1968, *Diopatra mexicana* n. sp., *Diopatra obliqua* Hartman, 1944, *Diopatra ornata* Moore, 1911, *Diopatra splendidissima* Kinberg, 1857. *Kinbergonuphis cedroensis* (Fauchald, 1968), *Kinbergonuphis pulchra* (Fauchald, 1980), *Mooreonuphis nebulosa* (Moore, 1911), *Mooreonuphis pumae* n. sp., *Onuphis eremita parva* Berkeley & Berkeley, 1941, and *Onuphis vexillaria* Moore, 1911.

POLYCHAETA (HARD BOTTOMS) FROM THE CHAFARINAS ISLANDS (SPAIN). *LOPEZ, E. & SAN MARTIN, G.* — (Departamento de Biologia, Unidad de Zoologia, Facultad de Ciencias, Universidad Autonoma de Madrid, Canto Blanco, 28049 Madrid, Spain). — The Chafarinas Islands are a very small Spanish archipelago in the Mediterranean Sea, placed in front to Morocco and Algeria borderline. These islands are almost uninhabited so they are very well preserved. Because of their location in the Mediterranean Sea, both Atlantic and Mediterranean influences can be expected, but no studies have been made on benthic fauna. A project for the study of benthos of hard bottoms is being made at present, suported by a grant of the "Comision Interministerial de Ciencia y Tecnologia". In this contribution, we present the results of the first year of resarch. A provisional list of about 130 species of polychaetes identified until now is given. Also two schematic profiles of typical hard-bottom communities at the Chafarinas Islands are given. Descriptions of two new species are being prepared. The description of *Exogone (Parexogone)* sp., that has been found also in the Italian coasts, is being made in collaboration with Drs. P. LANERA & P. SORDINO. *Pionosyllis* sp. has been found only in Chafarinas Islands.

ERRANT POLYCHAETES FROM THE CAPE VERDE ISLANDS. *LOPEZ, E. & SAN MARTIN, G.* — (Departamento de Biologia, Unidad de Zoologia, Facultad de Ciencias, Universidad Autonoma de Madrid, Canto Blanco, 28049 Madrid). — In August, 1985 the "I Expedicion Ibérica" to the Cape Verde Islands was undertaken. In that expedition samples of algae and sand for the study of some invertebrate taxa, among them the Polychaeta, were collected. The list of collecting stations and a map with their locations are given. In this contribution we present the results of the studies of the "errant" families of polychaetes. Seventy two species, belonging to 15 families, are recorded; 37 species are new records for the Cape Verde Islands, 12 of them are, furthermore, new to the region of the East Atlantic between Canary Islands and the Gulf of Guinea. A new species of *Dentatysyllis* Perkins, 1981 is described. Other interesting species, all them new records for the Cape Verde Islands, are *Acholoe orbiculata* Treadwell, 1921; *Lumbrineris crassidentata* Fauchald, 1970; *Opysthosyllis viridis* Langerhans, 1879; *Mirianida* sp.; *Syllis corallicoloides* Augener, 1924; *Eusyllis kupfferi* Langerhans, 1879; *Pionosyllis gesae* Perkins, 1981; *P. spinisetosa* San Martin, 1990; *P. procera* Hartman, 1965; *Exogone (Exogone) lourei* Berkeley & Berkeley, 1938; *Exogone (Sylline) naidinoides* Westheide, 1974 and *Sphaerosyllis magnidentata* Perkins, 1981.

WHY DO A FEW POLYCHAETE FAMILIES ACCOUNT FOR SO MANY POLYCHAETE GENERA? *MCHUGH, D. & FONG, P.P.* — (Biology Board, University of California, Santa Cruz, CA 95064, U.S.A.). — Within most taxonomic assemblages one or a few taxa dominate in terms of numbers of subtaxa. Recently, MARZLUFF & DIAL (1991) suggested that non-random patterns in taxonomic domination may be linked to life history traits that promote speciation and reduce extinction rates, i.e., short generation time and high resource availability. We investigated the phenomenon of taxonomic domination in the class Polychaeta. The class has about 80 families, 1,000 genera, and 7,000 species. The family Polynoidae accounts for > 8 % of all polychaete genera, and almost 30 % of all genera belong to just five of the 80 polychaete families (Polynoidae, Ampharetidae, Terebellidae, Syllidae and Serpulidae). Data for several genera in 20 families were collected on body size, egg size, fecundity, age at first reproduction, and life span. There is no significant correlation between body size and taxonomic diversity of families. Dispersal potential, as interpreted from egg size, also fails to explain the observed pattern of taxonomic domination. Our results indicate that there are significant negative correlations between age at first reproduction and life span, and the diversity of polychaete families.

NEW RECORDS OF THE TEREBELLID AULOPHORE LARVAE FROM THE FRENCH COASTS. *MARCANO, G. & BHAUD, M.* — (Laboratoire d'Océanographie Biologique, 2 rue du Professeur Jolyet, 33120 Arcachon, France). — Planktonic Terebellid larvae collected in the Bay of Banyuls (Western Mediterranean) are accorded to the genus *Loimia*. The term aulophore describes a pelagic larval stage bearing a transparent tube. These larvae, regularly observed since many years, were wrongly reported to be *Lanice conchilega*. The presence of a very large gelatinous tube without a well defined form in *Loimia* and the presence of a smaller, more rigid and well outlined gelatinous tube in *Lanice* is the main difference between the two genera. Other distinctive features are the pattern of the ocular spots, the body shape and the type of uncinial plates. Some specimens of a third larval type, already described for the French Atlantic coast as *Lanice* sp. have

Source : MNHN, Paris

also been observed. Only *L. conchilega* has been recorded from the numerous benthic samples taken in these areas, thus the recording of two new types of Terebellid aulophore larvae confirms the value of taking planktonic larval samples in increasing the faunistic knowledge of a region. In addition, larval research is important in assessing the biogeographic area of a species as larval dissemination may prevent or allow mixing of species populations.

ADULT ABUNDANCE, RECRUITMENT AND MORTALITY IN A SERPULID POLYCHAETE COMMENSAL WITH FIRE CORAL IN BARBADOS. *Marsden, J.R.* — (The Bellairs Research Institute, St. James, Barbados). — The 7-spined morphotype of *Spirobranchus polycerus* appears to be an obligate associate of live coral, occurring most commonly on *Millepora complanata*. It is reproductively isolated from the 2-spined morphotype and is hermaphrodite, whereas the 2-spined form is gonochoristic. A study of adult abundance and net recruitment on single blades of coral show that these parameters are significantly lower at SMB, the northernmost of four reefs studied. At HB, the southernmost reef, variation in adult abundance depends largely on variation in mortality rather than recruitment. The converse is true at the other reefs. At Hs, variation in recruitment depends largely on variation in blade base perimeter, i.e. on space available for recruitment. At the other reefs variation in recruitment depends largely on variation in the availability of recruits, i.e. on the availability of settling larvae and the survival of juveniles. At SMB low adult abundance appears to be the consequence of a recruitment limited to the past 1-4 years, rather than 5-12 years as at other sites. This situation is consistent with a population extending northward along the west coast of Barbados and with colonization of northern reefs dependent upon a pool of larvae produced on southern reefs where larval availability is high. A study of the distributions of blade height and worm tube aperture diameter indicates that, although worms may live for up to 12-14 years, most of them do not survive for more than two years, due to the destruction of tall (old) blades of coral by wave action. Possibly, simultaneous hermaphroditism in *S. polycerus* may have co-evolved along with the commensal habit, since the latter results in a discontinuous distribution on a short-lived substrate, a situation commensurate with difficulty in achieving fertilization in the gonochoristic condition.

CHANGES IN POLYCHAETE POPULATIONS FOLLOWING TERMINATION OF A SLUDGE DISCHARGE LOCATED IN SOUTHERN CALIFORNIA. *Martin, A., Phillips, C.A., Dojiri, M. & Thompson, B.* — (City of Los Angeles, Hyperion Treatment Plant, Environmental Monitoring Division, 12000 Vista del Mar, Playa del Rey, CA, 90293, USA). — For thirty years the City of Los Angeles disposed digested sludge from the Hyperion Wastewater Treatment Plant through a submerged outfall into the Pacific Ocean. The sludge was discharged at the head of a submarine canyon located in Santa Monica Bay, an embayment of the southern California coastline. Changes in polychaete populations reflect environmental conditions before and after termination of the sludge discharge. Three undescribed species of *Ophyrotrocha* were most abundant prior to termination and decreased in abundance post-termination. Subsequently, other opportunistic species colonized and dominated the area as sediment conditions improved. Post-termination sediment conditions were characterized by lower levels of contaminants, such as sulfides, chlorinated hydrocarbons, and some trace metals. As conditions improved from degraded (very high contaminant levels) to polluted (high to moderate contaminant levels), *Capitella capitata* dominated the area. As recovery continued *Pectinaria californiensis* became the dominant polychaete, representing a benthic community transitional between polluted and natural conditions.

MACROINFAUNAL POLYCHAETES OF A MEDITERRANEAN, SHALLOW-WATER BAY: A HIERARCHICAL APPROACH. *Martin, D. & Palacin, C.* — (Centre d'Estudis Avançats de Blanes, Camí de Santa Bàrbara s/n, E-17300, Blanes, Girona, Spain). — Descriptive studies of the biosphere are organized hyerarchically by a series of successive integration levels. Among these levels, Ecology deals mainly with the Ecosystems, Communities and Populations. This hierarchical approach was applied to our investigations, using the Annelida Polychaeta as a biological descriptor: the entire bay was spatially mapped (ecosystem), some of their components (communities) were seasonally described and dynamics of single species (populations) were analyzed through time. The study was carried out in Alfacs Bay (Ebro River delta), a semi-enclosed shallow-water area which is located in the North-East coast of the Iberian Peninsula (North-Western Mediterranean 40° 33'-38' N, 0° 32'-44' E). Alfacs Bay can be characterized as a "paralic" environment (*sensu* Guelorget & Pertuisot, 1983). In the **ecosystem level,** the spatial pattern of the benthic communities of the bay was descrived and correlated with the environment. Four communities were identified: clean-sand, stressed-mud, deep central-mud and a boundary community (placed between the first two communities and the deep one). Seasonal patterns in clean-sand and stressed-mud communities were descrived and analyzed in relation with the environment in the **community level.** The former showed higher species richness and biomass, and a less fluctuant composition. The latter was mainly characterized by higher abundances (Autumn to Spring) followed by a practically total defaunation (early Summer). Finally, population dynamics of the two more representative Polychaeta species of the stressed-mud community, *Capitella capitata* (Capitellidae) and *Streblospio shrubsoli* (Spionidae), were analyzed in the **population level.** Both were opportunistic species, with annual life-cycles and constant recruitment (lower in winter) in the bay. A single population of *S. shrubsoli* (production of 7.16 g. $m^{-2}$, average biomass of 4.10 g. $m^{-2}$, and P/B of 1.99), and two different populations of *C. capitata* (productions of 2.90 and 20.76 g. $m^{-2}$, average biomasses of 0.38 and 5.06 g. $m^{-2}$, and P/B of 7.70 and 4.10, respectively), were identified and followed annually. The population level involves certain degree of simplification, because dynamics of a single-species population is always related to, and controlled by, the

Source : MNHN, Paris

other components of the community. Nevertheless, one must consider it as a good tool to quantify, permiting to go back towards a more precise view of the community and ecosystem levels.

COMPARATIVE FEEDING BIOLOGY OF TWO VICARIOUS SPECIES OF THE *MACOMA BALTHICA* COMMUNITY, *NEREIS VIRENS* AND *HEDISTE (NEREIS) DIVERSICOLOR*. *Masson, S., Olivier, M., Desrosiers, G. & Retière, C.* — (Centre d'Océanographie de Rimouski, Département d'Océanographie, Université du Québec à Rimouski, 310 allée des Ursulines, Rimouski , Québec, Canada G5L 3A1). — A study on sharing out trophic ressources have been realized on two vicarious species of the *Macoma balthica* tidal flat communities, *Nereis virens* from the lower St Lawrence estuary (Canada) and *Hediste diversicolor* from the bay of Mont Saint-Michel (the English Channel). The species gut contents analysis revealed that both diet varies with field conditions and also individual ages. Juveniles of both species are essentially deposit feeders and *N. virens* adults are almost exclusively carnivorous. Diet temporal variations which are observed in the different habitats showed opportunistic features of these nereidians. It could play an important part in the mixing mechanisms of the particulate organic matter. *N. virens* adults, throughout the predatory relationship and cannibalism are susceptible to occur in the regulation of the population of this oligospecific estuarine community.

TEMPORAL CHANGES IN THE POLYCHAETE COMMUNITY AT AN ABANDONED SALMON FARM SITE. *Miller Retzer, C.L.* — (Department of Biology, University of Victoria, P.O. Box 1700, Victoria, B.C. V8W 2Y2 Canada). — The polychaete community was studied at an abandoned salmon farm site (following 2.5 yrs of operation) at Village Bay, Quadra Island, British Columbia. Benthic samples were collected for macrofauna and sediment analyses six wks, six months and one yr following closure of the facility. Initially the polychaete community at the farm was dominated almost exclusively by one capitellid species. After six months this species continued to dominate, but after one year the numbers approached those recorded at the reference station. Although species richness at the farm site increased during the course of the study it was lower than the reference station after one year. Analysis of sediment TOC and TON concentrations also indicated that partial recovery had taken place after one year of abandonment. Data analyses are ongoing with the ABC method (abundance, biomass comparison; Warwick, 1986), multivariate analyses and comparison of functional (trophic) groups; but preliminary results based upon 95 % of the total individuals (113 species) indicate that the polychaete community at the abandoned farm site changed very rapidly over the six months to twelve months period. After one year the farm site supports a transitional community which is characteristic of the "transitional zone" described by Pearson & Rosenberg's (1978) SAB diagram (of community changes in a gradient of organic enrichment): low to moderate richness, low biomass and low to moderate abundance.

DISTRIBUTION OF THREE NEREID POLYCHAETES IN RELATION TO SULFID CONCENTRATION WITHIN THE SEDIMENT IN DANISH COASTAL WATERS. *Miron, G. & Kristensen, E.* — (Institute of Biology, University of Odense, Campusvej 55, DK-5230 Odense, Denmark). — Results from field data (Kerteminde Fjord and Vellerup Vig, Denmark) suggested that hydrogen sulfid in the sediment influence the spatial distribution of the nereid polychaetes *Nereis virens, N. succinea* and *Hediste diversicolor*. Analysis showed that *N. virens* is confined in low sulfidic areas while *N. succinea* is found in high sulfidic sediments. *H. diversicolor*, on the other hand, showed a broader distribution in respect to hydrogen sulfid. Laboratory tank-experiments, however, indicated that all three species prefered non-sulfidic sediments in allopatry conditions. Preliminary results also showed that *H. diversicolor* was excluded from the tanks non-sulfidic side in sympatry conditions with each of the other two species. *N. virens* equally shared the non-sulfidic side with *N. succinea*. However, in these conditions, only *N. succinea* was found in the sulfidic portion of the tank. Overall, *N. virens* was the least tolerant species while the other two species showed some sort of adaptation in regard to sulfidic conditions. Results finally illustrated that competition between *H. diversicolor* and the other two species was high, particularly with *N. succinea*. Differences between field data and results from the laboratory tank-experiments, however, suggest that the distribution of *N. succinea* may also be dependant on other factors.

POLYCHAETE DISTRIBUTION AND COMMUNITY STRUCTURE ALONG A SALINITY GRADIENT (CANAL DE MIRA, RIA DE AVEIRO, PORTUGAL). *Moreira, M.H., Figueira, E. M. & Cunha, M. R.* — (Universidade de Aveiro, Campo de Santiago, 3800 Aveiro, Portugal). — The species composition and structure of the polychaete community of Canal de Mira (Ria de Aveiro) were studied. Four seasonal sampling surveys were carried out between December 1985 and September 1986. At each survey, samples were collected in a total of 40 stations (21 intertidal, 19 subtidal), distributed over 13 transects covering a distance of 21 km and a salinity range from 35 P.S.U. to 0 P.S.U. A total of 47 species were recorded. Structural indices (number of species, density and Shannon-Wiener diversity index) were determined for each station and sampling occasion. A cluster analysis was performed using Morisita similarity index. For each of the five groups of stations suggested by this analysis, the polychaete community was characterized using the average values of the structural indices (average number of species per station and sampling occasion = AVS; average number of individuals per square meter = AVD; average diversity = AVH') as well as the constancy, fidelity and relative dominance of the species present. In intertidal and shallow areas at the lower reaches of the channel (Group A), with fine sediment and high salinity, the number of individuals and species and the diversity is high (AVS = 12.1; AVD = 1,459.6; AVH' = 2.26) and the polychaete community shows low dominance of the most abundant species (*Heteromastus filiformis, Tharyx marioni, Owenia fusiformis*). In deeper areas with coarser sediment and more intense hydrodynamic conditions (Groups E

Source : MNHN, Paris

and B), the impoverished community (Group E: AVS = 2.4, AVD = 38.3, AVH' = 0.93; Group B: AVS = 4.6, AVD = 263.3, AVH' = 1.33) is strongly dominated by one species (*Nephthys cirrosa* and *Scoloplos armiger* respectively). In the middle and inner sections of the channel (Subgroups C1 and C2 and Group D), with high tidal and seasonal salinity variation, diversity, species richness and abundance gradually decline (Subgroup C1: AVS = 5.3, AVD = 1451.8, AVH' = 1.04; Subgroup C2: AVS = 3.2, AVD = 769.3, AVH' = 0.99; Group D: AVS = 1.0, AVD = 289.5, AVH' = 0.0) and the community becomes strongly dominated by euryhaline species (*Hediste diversicolor* and *Amage adspersa*). The results point out the influence of both salinity and hydrodynamic conditions as the main structuring factors of the polychaete community.

NOTEWORTHY COLLECTION RECORDS OF POLYCHAETES FROM ESTUARINE AND NEAR COASTAL WATERS OF THE U.S. MID-ATLANTIC REGION. *Mountford, N.K., Morris, C.T. & Arcuri, S.L.* — (Cove Corporation, 10200 Breeden Rd., Lusby, MD, 20657, USA). — Noteworthy collection records of polychaetes from coastal waters of the U.S. mid-Atlantic region are presented. These include: (1) northern or southern range extensions for eight species, (2) the first report of two species from the east coast of North America, and (3) the discovery of three species new to science. The significance of this presentation is to disseminate useful taxonomic information to the scientific community.

EVIDENCE OF A CADMIUM BINDING PROTEIN IN *ALLOLOBOPHORA CALIGINOSA* (ANNELIDA, OLIGOCHAETA): DISTINCTION FROM METALLOTHIONEINS AND HOMOLOGIES WITH HEMERYTHRINS. *Nejmeddine, A., Baert, J.L., Sautière, P. & Dhainaut-Courtois, N.* — (Université Cadi Ayyad, Faculté des Sciences de Marrakech I, Morroco). — Among annelids, earthworm oligochaetes generally show a good tolerance for heavy metal contaminants and, to the best of our knowledge, only metallothioneins (MTs) have been reported to play a role in the detoxification process (Morgan *et al.*, 1989). Previous studies have showed that the oligochaete *A. caliginosa*, collected from the sewage spreading fields in the city of Marrakech (Morroco), presents a good tolerance to heavy metals and accumulates high level of Cd, Zn and Cu (Sedki, 1990). We have thus investigated the detoxification mechanisms in this species. Following gel filtration chromatography on Sephadex G75, one Cd-binding peak was detected in an extract from *A. caligino*sa contamined with cadmium. Two subsequent cation-exchange chromatograhies allowed the purification of Cd-binding protein which was called Cd-BP14. This protein is a monomer with a molecular weight of 14 kDa and has an isoelectric point of 6.5. Althrough this molecular weight is rather similar that of MTs, a comparison of the amino acid composition revealed several major differences. Indeed, while MTs have a high cystein content (>30 %), cystein was present in Cd-BP 14. Futhermore, CD-BP 14 contains a high level of aromatic acids (11 %) and histidine (6 %), amino acids not present in MTs. A marked difference also occured between Cd-BP 14 and MTs when the level of bound metal was compared. On the basis of these results we conclude that Cd-BP 14 is different from metallothioneins described in mammals or other invertebrates. To our knowledge, such a Cd-binding protein has never been described in oligochaete annelids.On the basis of the characteristics described above, Cd-BP 14 is similar to an Cd-binding protein (MP II) isolated from an annelid polychaete *Hediste diversicolor* (Nejmeddine *et al.*, 1988). This analogy was confirmed by the determination of the first 33 amino acids at the NH2 extremity of Cd-BP 14 which revealed 61 % homology with the N-terminal part of MP II (Demuynck *et al.*, 1991). The N-terminal sequence of Cd-BP 14 shares also 40 to 65 % homology with that of sipunculid hem erythrins, non-heme iron-binding proteins. This homology with hemerythrins was confirmed on the basis of characteristics including molecular mass, iron content UV/visible spectrum, amino acid composition and immunological cross-reaction using antibody against Cd-BP 14. Homology between hemerythrins and MP II from *H. diversicolor*, marine animal, has been described (Demuynck *et al.*, 1991). By contrast, to our knowledge, it is the first time that homology between hemerythrins and a protein from a terrestrial animal is reported.

TROPHIC RELATIONS BETWEN POLYCHAETOUS ANNELIDS AND BRACHYURAN CRABS IN THE SOUTHERN BRAZILIAN COAST. *Nonato, E.F, Petti, M.A.V. & Paiva, P.C.* — (Instituto Oceanografico, Universidade de Sao Paulo, Praça do Oceanografico, 191-05508, Sao Paulo, SP, Brazil). — The polychaetous annelids constitute an important feeding resource for several species of the benthic and demersal marine fauna. The group is of particular interest since through the family recognition it is possible to obtain various information regarding their feeding behavior and motility: detritivores (deposit and suspension-feeders) are generally sessile or discreetly motile, carnivores and omnivores normally have greater locomotion capabilities. Considering that the brachyuran crabs are the main megabenthic group and the polychaetes the main macrobenthic group in the studied area, their inter-relations are fundamental to the understanding of the local trophic web. In this way the contribution of the polychaetes to the diet of the main brachyuran crabs species was studied on the inner shelf (between 10 and 42 meters depth). 2.715 stomachs belonging to six species (*Persephona mediterranea, Portunus spinimanus, P. spinicarpus, Callinectes ornatus, Hepatus pudibundus* and *Libinia spinosa*) were analysed. Out of 1,815 stomachs whose contents were indentifiable, 513 had polychaetes, with considerable variations between the different species. Notwithstanding the identification of the feeding content in brachyuran crabs being made difficult by the process of ingestion and trituration, regarding the polychaetes the task is facilitated by the presence of certain structures more resistant to digestion such as setae, uncini, hooks, mouthpieces and opercula. 30 families, 15 genus and five species were determined. 28.6 % of the polychaetes encountered could not be identified. 26.6 % were carnivores, mainly of the order Eunicida; 39.9 % were deposit-feeders, mainly Capitellidae, Maldanidae and Terebellidae; 3.6 % were suspension-feeders (families Sabellidae and Serpulidae) and

Source : MNHN, Paris

1.3 % were omnivores. In *Persephona mediterranea* the greatest occurrence of polychaetes was found (in 80.3 % of the stomachs). The deposit-feeders, the most abundant polychaete trophic group in the area, where the commonest food item for the brachyuran crabs, except for *Portunus spinicarpus* and *Callinectes ornatus* in the stomachs of which the carnivores were more important; this, probably, owing to a great predating capability of these agile Portunidae.

NEW RECORDS AND ZOOGEOGRAPHICAL STUDY OF THE FAMILY NEREIDIDAE FROM CANARY ISLANDS. *NUNEZ, J.* — (Facultad de Biologicas, Departamento de Biologia Animal, Universidad de La Laguna, 38206 La Laguna, Tenerife, Canary Islands, Spain). — The family Nereididae is represented in the Canary Islands by three subfamilies, Nothophycinae, Namanereidinae and Nereidinae, and 18 species belonging to nine genera. *Micronereis* (one spec.), *Lycastopsis* (one spec.), *Websterinereis* (one spec.), *Rullierinereis* (one spec.), *Nereis* (two spec.), *Neanthes* (four spec.), *Ceratonereis* (two spec.), *Perinereis* (four spec.) and *Platynereis* (two spec.). In this paper, three species previously unknown from Canarian waters are recorded, *Neanthes fucata* (Savigny, 1820), *Ceratonereis vittata* Langerhans, 1884 and *Platynereis coccinea* (Delle Chiaje, 1841). Juvenile specimens of *Nereis funchalensis* (Langerhans, 1880) are described; they are very similar to *N. jacksoni* Kinberg, 1866 (HUTCHINGS & TURVEY, 1982). *Perinereis taorica* Langerhans, 1881 is redescribed from 15 specimens, from Puerto de la Cruz, the type of this species described from the same area having been lost. In addition, a illustrated key and zoogeographical analysis of the family is maked.

COMPARATIVE STUDY OF THE PROVENTRICULUS IN FOUR SPECIES OF SYLLINAE (POLYCHETA, SYLLIDAE). *OCANA, O., NUNEZ, J. & TALAVERA, J. A.* — (Facultad de Biologicas, Departamento de Biologia Animal, Universidad de La Laguna, 38206 La Laguna, Tenerife, Canary Islands, Spain). — The proventriculus is used as taxonomic character in the family Syllidae (size, morphology and number of the muscle cell rows). Nevertheless, these studies are usually about external morphology. A proventriculus morphology-microscopy study is given for four representative species of syllids collected in Canary Islands (*Haplosyllis spongicola, Syllis amica, S. gracilis* and *S. armillaris*).

ECOLOGICAL DISTRIBUTION AND SEASONAL VARIATION OF SUBTIDAL POLYCHAETES POPULATIONS IN THE MONDEGO ESTUARY (PORTUGAL). PARDAL, M. A., MARQUES, J. C. & BELLAN, G. — (Departamento de Zoologia, Fac. Ciências e Tecnologia, Universidade de Coimbra, 3049 Coimbra Codex, Portugal). — The Mondego estuary is under severe environmental pressure, essentially due to human activities. It consists of two arms, north and south, with very different hydrographic characteristics. The north arm, which is the location of Figueira da Foz harbor, is deeper, while the south arm is almost silted up in the upstream areas. This causes the fresh water to flow essentially by the north arm, while the circulation in the south one is mostly due to tides and to the usually small fresh water input of a tributary, the Pranto river. In addition, due to differences in depth, the tidal penetration faster in the north arm, which causes daily changes in salinity to be much stronger, whereas daily temperature changes are higher in the south arm. The type of substrate is also clearly different in both estuarine arms. In the north one bottoms are mainly composed of medium to coarse sand, with low fractions of organic matter, while muddy bottoms with higher fractions of organic matter are predominant in the south arm, particularly in the upstream areas. Fine to medium sand bottoms can also be find in downstream areas of the south arm. Despite of the increasing environmental pressure, there was no reference data on the Mondego estuarine system until 1985, namely for the biological communities, from which the impact of human activities over the structure and functioning of the ecosystem could be assessed. From 1985 to 1990 a general survey of the benthic communities was carried. The aim was to characterize the macroinvertebrate communities structure in relation to the physical and chemical environmental parameters and to identify the most important species in the observed structure (number of individuals and biomass), which might have a key role in the ecosystem functioning. The present paper was based on data from a sampling program over the subtidal communities carried out from December 1989 to September 1990. Samples provided about 4,800 polychaetes from 20 species. *Amage adspersa* was the most abundant species (maximum of 4,115 ind. $m^{-2}$ in June 1990), representing 79.8 % of the sampled specimens. However, it was found almost exclusively in the south arm of the estuary and in the Pranto river. *Streblospio shrubsolii* was the second most abundant species (9.8 % of the sampled specimens) being found in all the studied area. *Capitella capitata* and *Polydora ciliata*, both considered as indicators of organic pollution, were found only in the south arm and in the Pranto river. *Hediste diversicolor* was found almost only in the upstream areas of the north arm, presenting relatively small densities (maximum of 464 ind. $m^{-2}$). A comparison with previous data allowed to think that it is decreasing both in density and area of distribution. Nevertheless, this fact needs further confirmation. Five species, *Nephtys cirrosa, N. longosetosa, N. hombergi, Eulalia* sp., and *Lagis koreni* were found only near the mouth, were the marine influence is stronger. Species richness changed seasonally, with a maximum in the summer (14 species in September) and a minimum in the winter (eight species in March). The highest populations densities were found in late spring (June) (54.6 % of the total number of individuals sampled). Species richness and population densities were clearly lower in the north arm, mainly due to bottom disturbance related to the harbor facilities, and probably to strongly daily variations in water parameters. The south arm, where the circulation depends mainly on tides, despite of more organic pollution, lower dissolved oxygen levels, and higher nutrients concentrations in the water, still presents higher species richness and populations densities. In a general way, the species richness in the Mondego estuary is low in comparison with data from other studied estuarine systems.

Source : MNHN, Paris

*PSEUDOCIRRATULUS KINGSTONENSIS* AUGENER, 1922: NOT A CIRRATULID BUT AN ANNELID OF UNCERTAIN AFFINITIES (POLYCHAETA?: PSEUDOCIRRATULIDA NEW ORDER, PSEUDOCIRRATULIDAE NEW FAMILY). *PETERSEN, M.E.* — (Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen 0, Denmark). — *Pseudocirratulus kingstonensis* Augener, 1922, from the intertidal zone of the West Indies, is an earthwormlike species described from a few large specimens questionably assigned to the polychaete family Cirratulidae. No filamentous appendages of any kind were observed, and all setae were reported to be gently curved unidentate hooks. The species has been known only through the brief, unillustrated original description, the correctness of which has been doubted. A reexamination of the types and of a nontype specimen recently found in the collections of the Zoological Museum, University of Copenhagen, has revealed that the species is correctly described but not a cirratulid or referable to any known family or order of polychaetes; although not an oligochaete (e.g., the gut is simple and not specialized; none of the specimens have a clitellum; there are no reproductive organs of oligochaete type), it is most likely to be confused with earthworms (Oligochaeta: suborder Lumbricina). The species is figured for the first time, redescribed and transferred to the Pseudocirratulidae, new family of the new order Pseudocirratulida. A lectotype is designated and the affinities of the species, family and order are discussed.

HERMAPHRODITIC CIRRATULIDS (ANNELIDA, POLYCHAETA) FROM DANISH WATERS, WITH NOTES ON EARLY DEVELOPMENT, DESCRIPTION OF A NEW SPECIES OF *APHELOCHAETA* BLAKE AND REVIEW OF HERMAPHRODITISM AMONG THE CIRRATULIDAE. *PETERSEN, M.E.* — (Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen 0, Denmark). — Three species of Danish Cirratulidae are known to be hermaphroditic. *Tharyx vivipara* Christie, 1984, originally described from estuaries of northeast England, and *Caulleriella fragilis* (Leidy, 1855), originally described from under stones at Point Judith, Rhode Island, U.S.A., are newly reported from Danish waters. *Aphelochaeta* new species, is new to science. All three species are described and figured and a key to known species of *Aphelochaeta is* provided. *Tharyx vivipara* is infaunal, whereas both *C. fragilis* and *Aphelochaeta* n.sp. are cryptofaunal, occurring in crevices in dead mollusc and barnacle shells and other calcareous matter in *Laminaria* holdfasts and similar habitats. At least *Aphelochaeta* n.sp., and perhaps also *C. fragilis*, brood their young. Some early stages of both species are described and figured, and *C. fragilis* is differentiated from *C. viridis* (Langerhans, 1880) and *C. bioculata* (Keferstein, 1862), similar species with which it has been confused. The status of *Caulleriella bioculata parva* Gillandt, 1979 and *Tharyx multibranchis* (Grube, 1863) is commented. Hermaphroditism among the Cirratulidae is reviewed and it is suggested that the phenomenon is probably more widespread among Polychaeta than usually realized. Some problems of dispersal for species with direct development and brood care are pointed out.

ABUNDANCE DYNAMICS OF MEROPLANKTONIC POLYCHAETE LARVAE AT "HELGOLAND ROADS" (GERMAN BIGHT). *PLATE, S. & HUSEMANN, E.* — (AG Entwicklungsphys. d. Tiere, Lehrstuhl f. Spez. Zool. & Parasitol., Ruhr-Universität Bochum, Postfach 10 2148, D-W-4630 Bochum 1, Germany). — During a three year plankton monitoring at the island of Helgoland (German Bight, North Sea) a total of 212 quantitative plankton samples were collected by horizontal, surface-near hauls twice a week. We observed meroplanktonic polychaete larvae of 57 species out of 22 families. With 15 and height species, respectively, the families Spionidae and Phyllodocidae were the most dominant members of the polychaete plankton. Highest larval abundances occurred in *Lanice conchilega* (Terebellidae) with 8,870 ind. $m^{-3}$, *Magelona mirabilis* (Magelonidae) with 5,424 ind. $m^{-3}$, *Malacoceros fuliginosus* (Spionidae) with 5,250 ind. $m^{-3}$ and *Polydora ciliata* (Spionidae) with 1,170 ind. $m^{-3}$. Since the presence of meroplanktonic larvae is a criterion of reproduction, it is possible to make some conclusions on the timing of reproduction. The meroplanktonic larvae of some species occurred over more than six months in the plankton of "Helgoland Roads". Examples for species with a semi-continuous reproduction are *Polydora ciliata* (larvae from February to September), *Laonice cirrata* (Spionidae) (larvae from May to February) and *Lanice conchilega* (larvae from February to November). Larvae of *P. ciliata* were continuously present during the whole breeding season, but we recognized two or three main reproductive phases, characterized by increased larval abundance. Field studies showed a distinct temperature dependence of larval development. At water temperatures between 1 and 4.5 °C, larval development from the first planktonic stage with three setigers to the 12-setiger stage took about 70 days. At temperatures from 8 to 11.5 °C, only 27 days were needed to reach the same stage. Short larval appearance, which points to reproduction with distinct gamete releases, was recognized for *Eulalia viridis* (Phyllodocidae), *Eteone longa* (Phyllodocidae), *Scoloplos armiger* (Orbiniidae), *Polydora flava* (Spionidae) and some other species. In many cases, the onset of reproduction showed a temperature dependence. In *S. armiger*, *E. viridis* and *E. longa* low winter temperatures led to a delayed reproduction. The reproduction of *P. flava* was found to be adapted to high water temperatures. Larvae, first occurring in the plankton at the 6-setiger stage, could be observed in August and September. At this time, temperature reaches its maximum. The occurrence of the larvae was always restricted to a period of four weeks. This points to a synchronized reproduction and a short pelagic development. *Pomatoceros triqueter* (Serpulidae) is known for producing ripe gametes throughout the year. During the present study larvae occurred only between the end of July and the end of October. Reproduction always started at temperatures above 13 °C. The pattern of larval records pointed to the release of several batches of gametes, which followed a lunar or semi-lunar rhythm.

PHYLOGENY OF *PHYLLODOCE* (POLYCHAETA-PHYLLODOCIDAE). *PLEIJEL, F.* — (Natur-historiska Riksmuséet, Box 50007, S-104 05 Stockholm, Sweden). — The phylogeny of thirteen species of the polychaete genus *Phyllodoce* is

Source : MNHN, Paris

estimated with 26 unordered morphological characters and 60 character states. The genus is large (over one hundred nominal species) with many poorly known members and the analysis is based on a small selection only. Following recent, higher-level phylogenetic studies *Chaetoparia nilssoni* and a selection of *Paranaitis*-species were chosen for outgroups. Six equally parsimonious trees with a CI of 0.79 were obtained. The data set is examined for cladistic structure in a permutation tail probability test, the result of which clearly indicate presence of non-random, hierarchical pattern. The genus is reclassified and divided in three subgenera: *Phyllodoce*, *Zverlinum*, *Anaitides*, and the hypothesized synapomorphies are used for subgeneric allocation of the remaining species in the genus.

EFFECT OF FOOD QUANTITY ON GROWTH AND REPRODUCTIVE CHARACTERISTICS OF *CAPITELLA* SP. (ANNELIDA, POLYCHAETA). *Qian, P.Y. & Chia., F.S.* — (Department of Zoology, University of British Columbia, Vancouver, B. C., Canada V6T 1Z4). — Effects of food quantity on growth, fecundity (defined as number of eggs deposited in the first spawning), egg size, egg energy content, and total reproductive output (total egg volume or total energy invested in spawned eggs) of *Capitella* sp. were examined in the laboratory. Results indicate that food quantity affected fecundity, egg size, egg energy content, and total reproductive output of *Capitella* sp. Fecundity increased with increasing food quantity, whereas egg size and egg energy content decreased with increasing food quantity. These results suggest that there is a trade-off between fecundity and egg quality (in terms of egg size and egg energy content), thus supporting the hypothesis that when food-limited, polychaetes produce fewer, but higher quality offspring. Results further show that *Capitella* sp. is very sensitive to change in food quantity. Minor changes in food quantity (< 0.1 mg dry *Ulva*. worm$^{-1}$. day$^{-1}$) gave rise to measurable changes in fecundity and egg size, suggesting that life history characteristics in *Capitella sp.* is flexiable and can be easily modified by environmental factors, such as food quantity.

*IN SITU* MEASUREMENT OF RECRUITMENT, MORTALITY, GROWTH, AND FECUNDITY OF *CAPITELLA* SP. (ANNELIDA, POLYCHAETA). *Qian, P.Y. & Chia, F.S.* — (Department of Zoology, University of British Columbia, B. C. Canada). — Recruitment and mortality of post-larval stages of *Capitella* sp. were determined *in situ* at two sites near Bamfield Marine Station, B. C. Recruiting rates of juveniles into settling trays placed in the mid-intertidal region were not significantly different at the two study sites, even though larval abundance at one site was about one order of magnitude higher than that of the other site. This suggests that recruitment in these areas is not affected by larval abundance. Mortality rate (% loss x day$^{-1}$) was more than 3 % for young juveniles (body volume < 3 mm$^3$) and less than 0.3 % for larger than ones (>10 mm$^3$). These indicate that juvenile mortality governs directly recruitment pattern and population dynarnics in our study area. A method of marking polychaetes with vital dye was introduced and this enabled us to follow the growth and reproduction of *Capitella* sp. in the field. Growth rate of marked sibling individuals measured *in situ* was similar to that of laboratory reared animals. Marked sibling juveniles were succesfully raised *in situ* to sexually maturity and their reproductive characteristics measured. Among 147 females developed from the marked sibling juveniles of a single spawning, 142 individuals produced small numbers of large eggs. On average, each animal produced 764 ± 207 (N = 42) eggs x spawning$^{-1}$; each egg measured 7.3 ± 0.01 x 10$^{-3}$ mm$^3$, and contained 88 ± 9.5 microjoules energy. These large egg developed into lecithtrophic larvae in the adult's tube. The other five females produced small eggs that measured 0.63 ± 0.40 x 10 10$^{-3}$ mm$^3$, contained 8.6 ± 1.56 microjoules energy, and developed into planktotrophic larvae that had a pelagic larval life of 2-3 weeks. Mean fecundity of these five individuals was 6,890 ± 3,116 eggs x spawning$^{-1}$. Plasticity of life-history strategy of *Capitella*, which has been demonstrated in the previous laboratory studies, was confirmed in the field.

THE LIFE HISTORY OF THE POLYCHAETOUS ANNELID *HALOSYDNA JOHNSONI*. *Reish, D.J. & Rossi, M.M.* — (Department of Biology, California State University, Long Beach, California 90840-3702, U.S.A.). — The life cycle of the polynoid polychaete was completed under laboratory and field conditions. Both eggs and sperm were shed free into the water through the nephridial papillae. The fertilization membrane appeared shortly thereafter with the first cleavage occurring in one hour. Additional division were rapid at 18° C with a swimming blastula present at four hours. The trochophore with eyespots was observed at 24 hours and began to feed on phytoplankton at two days. Metatrochophore I stage was formed by seven days and consisted of seven segments. Metatrochophore II possessed setae, median antenna, anal cirri, eight segments, and four pairs of elytrae at 12 days. Metamorphosis occurred at day 14 at which time the larvae consisted of nine setigerous segments and five pairs of elytrae. Worms attained 26 segments at 40 days, 32 at 80 days, and 37, the adult number, at 100 days. Both sexes spawned at nine months. Settlement of juvenile worms in the field occurred throughout the year in southern California with peaks occurring in early spring and mid-summer. This is the first report of rearing a member of Family Polynoidae through sexual maturity in the laboratory .

SPACE OCCUPATION MODALITIES FROM THREE SPECIES OF TUBICULOUS INTERTIDAL NEREIDS: *HEDISTE (NEREIS DIVERSICOLOR)* O.F.MULLER, *NEREIS VIRENS* SARS AND *PERINEREIS CULTRIFERA* (GRUBE). *Retière, C., Desrosiers, G., Scaps, P. & Miron, G.* — (Laboratoire Maritime, 17 avenue George V, B.P 28, 35801 Dinard, France). — *Hediste diversicolor* and *N. virens*, two major components of the *Macoma balthica* oligospecific community, inhabits muddy sands in shallow estuarine soft-bottoms. *Perinereis cultrifera*, a widespread species, is found in particular biotops which correspond to zone of interface between heterogeneous sediments and rocky substrates. The distribution

Source : MNHN, Paris

modalities of individuals from these three species were studied in the Saint Lawrence estuary *(N. virens)* and in the English Channel, on the north coast of Brittany *(H. diversicolor* and P. *cultrifera)*. On an observation site scale (coves, intertidal zones), the dimensional structure and the population density of both *N. virens* and *P. cultrifera* vary with the bathymetry and certain sediment characteristics, juveniles occupying preferentially, in greater number, the highest levels. Differently, juveniles and adults of *H. diversicolor* coexist on the area occupied by the population. The first distribution type is probably the result of the swarming of epitokous individuals in flow period, leading to a passive (and may be active) transport of gravid individuals and/or sexual products of *P. cultrifera* and *N. virens* young larval stages (which pelagic life does not exceed a few hours) to the higher levels of the intertidal zone. A migration in an offshore direction, during the growth period, could control the structuring of the population. Inversely, the atokous reproduction of *H. diversicolor*, with the possibility of egg incubation within the galery inhabited by the female and the liberation of erpochaetes, restrains considerably the dispersion of the individuals. At small-scale, individuals of these three species are distributed in patches. Though individuals accept that their feeding area may be forage by congenerics of the same size, individuals defend harshly their territory, i.e., their galery which shape and size are related to density. The agonistic behaviour, expressed in the course of the burrow development within the substrat, appears to be an important factor in the regulation of populations. It also express itself, at least for *H. diversicolor*, in migrations, not related to reproduction or growth, in the water column and contribute to the dispersion of individuals which favors, when they return to the bottom, encounters between burrow occupants and intruders trying to enter a new burrow. In *H. diversicolor*, cannibalism between adults and juveniles could hold an non-negligible role. Thus, it appears that the space occupation modalities expressed by these three Nereid species are determined by the coupling between reproductive mechanisms and hydrodynamism and individual behaviour, the former exerting effects and the latter expressing itself at very different spatial scales.

AMPHARETIDAE (ANNELIDA, POLYCHAETA) FROM ANTARCTIC WATERS, ATLANTIC SECTOR. *ROSENFELDT, P.* — (Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Martin-Luther-King-Platz 3, 2000 Hamburg 13, Germany). — The study material was sampled during cruise ANT V/l of the German RV «Polarstern» to Antarctica from May to June 1986. The samples were obtained at 26 stations off the Elephant Island and the Antarctic Peninsular by van Veen Grab at 9-532 m. Eleven ampharetid species were found, of which ten were known before in the area: *Amage sculpta* Ehlers, 1908; *Ampharete kerguelensi* McIntosh,1880; *Amphicteis gunneri antartica* Hessle,1917; *Anobothrella antarctica* (Monro,1939); *Eusamythella sexdentata* (Hartman,1967); *Melinna cristata* (Sars, 1851); *Neosabellides elongatus* (Ehlers,1912); *Neosamytha gracilis* Hartman,1967; *Parampharete weddellia* Hartman,1971 and *Sosanopsis kerguelensis* Monro,1939. The 11 th species of the genus *Asabellides* was unknown to science and will be presented here with detailed illustrations. It is distinguished from congenus by different morphology of its gills, uncini, and lower number of abdominal segments (8-11). Two species inhabit the Antarctic/Subantarctic region, as well as waters of Southern S. America. Five species are endemic to Antarctica. One species is of cosmopolitan distribution. The remaining species inhabit the Antarctic region, as well as waters of South Africa. *M. cristata* was the most abundant species, with 185 individuals only at Station 142, at 466 m.

EVOLUTION OF REPRODUCTIVE MECHANISMS IN THE SABELLIDAE (POLYCHAETA). *ROUSE, G.W.* — (Department of Invertebrate Zoology, Smithsonian Institution, Washington D.C. 20560, U.S.A.). — Polychaetes have a great range of reproductive mechanisms. However the general assumption persists that polychaetes spawn small eggs and simply structured sperm into the sea-water; fertilization takes place in the water as does early development through a larval stage: the trochophore. These traits have consistently been viewed as primitive. In order to assess whether external fertilization, concomitant with "primitive" sperm (FRANZÉN 1956), small eggs and planktonic larvae, has been re-expressed (or "re-evolved") the study of monophyletic groups with various forms of reproductive methods should be informative. Recent rigorous cladistic analyses of the Sabellidae by FITZHUGH (1989, 1991) allow the possibility of testing hypotheses regarding the evolution of reproductive mechanisms. FITZHUGH (1989) re-defined two sub-families of sabellids, the Fabriciinae and the Sabellinae. Examination of the cladograms produced by FITZHUGH indicates a general trend of increasing size from small plesiomorphic fabriciins to large apomorphic sabellins. All of the Fabriciinae are continuous brooders of directly developing larvae. Sperm storage by females is indicated in every genus (ROUSE,1992). Plesiomorphic sabellins such as *Oriopsis* spp. are also small and have a similar reproductive mechanism to the Fabriciinae, though the homologies of reproductive structures are unclear. Intratubular brooding is rare in the more apomorphic sabellins. Broadcast spawning or extratubular brooding (with a dispersal phase) is found in all other genera, except for *Potamilla* and *Amphiglena*. The most apomorphic sabellins, *Eudistylia* and *Schizobranchia* are broadcast spawners. The sister group to the Sabellidae is the Serpulidae. KNIGHT-JONES & BOWDEN (1984) suggested that brooding is "primitive" for the Sabellida based on the idea that the Spirorbinae, all brooders, are the most primitive of the Sabellida. However ten HOVE (1984) and FITZHUGH (1989) have shown the spirorbins are the most apomorphic of the Serpulidae. Plesiomorphic serpulids, the Filograninae, do have intratubular brooding but species in other sub-families, apart from the spirorbins, have broadcast spawning and feeding trochophores. Careful examination of the breeding patterns in the Serpulidae is needed. The feeding trochophore of the serpulids may also be secondary. FITZHUGH's classification of the Sabellidae implies that broadcast spawning with non-feeding 'trochophores' have evolved from intratubular brooders with directly developing larvae. More data is needed on reproduction in the Sabellinae to properly understand this

Source : MNHN, Paris

development. Because of the increased-size trend in the Sabellidae phenomena such as paedomorphosis should be taken into account when examining character states in this family. For this reason studies on larval development are also needed.

REPRODUCTIVE STRUCTURES AND SYSTEMATICS OF THE FABRICIINAE (POLYCHAETA: SABELLIDAE). *ROUSE, G.W.* — (Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560, U.S.A.). — Males and females of at least one species from each of the following nine sabellid genera, *Augeneriella, Fabricia, Fabriciola, Fabricinuda, Novafabricia, Manayunkia, Parafabricia, Pseudofabriciola* and an undescribed new genus A (FITZHUGH *et al.* in preparation) were examined by light and electron microscopy. These genera, along with *Pseudofabricia aberrans*, currently comprise the sub-family Fabriciinae. The reproductive systems were examined in order to assess the proposed monophyly of this assemblage. Females of all species examined brood directly developing larvae within their tubes. Outgroup comparisons were made with the other sabellid sub-family, the Sabellinae and the Serpulidae. Males of species in all nine genera were found to have a dorsal, ciliated, sperm duct running directly beneath the faecal groove of the thoracic region. The sperm duct, containing only mature spermatozoa, terminated immediately behind the radiolar crown. No sabellins have this duct. It is also absent in members of the Serpulidae. All of the Fabriciinae have spermatids developing in large clusters of several hundred cells. Serpulids (except for spirorbins) and sabellins have sperm developing in tetrads. The Fabriciinae also have a sperm structure distinct from the Sabellinae and the Serpulidae. Within the family there were differences between genera in mature sperm structure. These differences, that could be useful in systematics, involved the structure of the sperm midpiece, elongation of the acrosome and the degree of coiling of the nucleus. Females of the species in the genera *Manayunkia* genus A, *Fabricia, Parafabricia* and some species of *Fabriciola* were found to have a pair of spermathecae associated with the radiolar crown or peristomium. Females in the remaining genera were found to have no specialized organs for sperm storage. Females of *Augeneriella* and *Fabricinuda* store sperm in epidermal cells of either the proximal inner surface of the radiolar crown or just inside the buccal cavity. The spermathecae of *Manayunkia*, some species of *Fabriciola* and genus A comprised of a simple blind duct lined with heavily pigmented cells. The spermathecae of *Fabricia* and *Parafabricia* were more complex with three distinct regions. The monophyly of the Fabriciinae *(sensu* FITZHUGH, 1989) is well supported by this analysis. A number of autapomorphies for the sub-family, based on reproductive characters are established. Genera originally in the Fabriciinae such as *Oriopsis* and *Chone* are clearly sabellins. The status of *Caobangia* is still unresolved and a close examination of this genus is warranted. Within the Fabriciinae it appears that *Fabriciola* will have to be split into two genera, one of which is the sister group to *Manayunkia*. Elucidation of the reasons for presence of spermathecae in some genera and not in others, when the other variables in the reproductive method are maintained, requires further investigation.

INTERACTIVE PROCESSES IN A *LANICE CONCHILEGA* (POLYCHAETA, TEREBELLIDAE) DOMINATED INTERTIDAL COMMUNITY. *ROWE, G.A., HAWKINS, L.E., HUTCHINSON, S., SHEADER, M. & HIRST, A.G.* — (Southampton University Department of Oceanography, Southampton, SO9 5NH, U.K.). — The benthic macrofauna and sediment at an intertidal midshore site on the eastern shore of Southampton Water, U.K. have been sampled for 12 months. The large tube building polychaete *Lanice conchilega* (Pallas) was the numerical and biomass dominant of the community. The density of *L. conchilega* varied both spatially across the region and temporally over the sampling period. Disturbance of the sediment, depletion of the percentage bioavailable protein and harsh climatic conditions were accompanied by declining faunal abundance and species richness during winter. The distribution of *L. conchilega* was, for the most part, contagious throughout the sampling period. Increased mortality of the population in February and March was less pronounced in dense patches giving a highly contagious distribution. Dense aggregations of tubes increased stability by resisting erosion and facilitating accumulation of sediment, bringing about local seasonal changes in topography. Major recruitment of young *L. conchilega* adults ( > 500 µm) was seen in June, and spawning has been estimated to occur as early as late March. Initial settlement and growth of recruiting individuals was more successful in areas of higher adult density. The numbers of animals and species richness have been positively correlated with the density of *L. conchilega* tubes. The study suggests that *L. conchilega*, through direct and indirect interactions, plays a major role in structuring the community at the site.

UPDATED CHECKLIST OF POLYCHAETES (POLYCHAETA) FROM THE GULF OF MEXICO, THE CARIBBEAN SEA, AND ADJACENT AREAS IN THE WESTERN ATLANTIC. *SALAZAR-VALLEJO, S.I.* — (Centro de Investigaciones de Quintana Roo, Apdo. Postal 424, 77000 Chetumal QR, México). — The only checklist of polychaetes from the tropical and subtropical Western Atlantic was published almost 20 yr ago (PERKINS & SAVAGE, 1975). Since then, some 40 new genera and almost 180 new species have been described; further there have been several modifications and suppresions so an updated list is really needed. By following PETTIBONE (1982) taxonomic array, there are now over 1,100 valid species recorded in 20 orders, 71 families and 423 genera. The list of references since 1975 is made of almost 130 works. In order to make this checklist as complete and useful as possible, and because my library might lack some important papers, any help or discussion will be appreciated.

SPATIO-TEMPORAL VARIABILITY OF POLYCHAETE POPULATIONS IN A SUBTIDAL ESTUARINE AREA. *SANCHEZ, A., MORA, J., GLEMAREC, M. & LASTRA, M.* — (Universidad de Santiago, Facultad de Biología, Departamento de Biología

Source : MNHN, Paris

Animal, 15706, Santiago de Compostela, Spain). — Environmental variability is an important cause of fluctuations in marine ecosystems. In order to assess the contribution of a particular environmental factor we need to know not only how strongly it is coupled to the biological components, but also how responsive the ecosystem is to fluctuations on that space-time scale. This study describes the results of polychaete spatial distribution studied in 48 sites at Ria de Ares-Betanzos (NW Spain) and one year monthly survey of two soft sediment stations at its estuarine inner part. The aims were to compare in a spatio-temporal scale the degree of biological organization of polychaete populations and the magnitude of variability due to environmental factors as sediment grain-size, organic matter and redox potential condition as well as to bottom water hydrological parameters (pH, salinity, temperature and oxygen contents). A *Diplocirrus glaucus-Stylarioides plumosa-Owenia fusiformis-Diopatra neapolitana* assemblage occurred at 3-15 m deep muddy fine sandy bottoms of the estuarine internal part with organic carbon values up to 3 % while *Aponuphis bilineata-Glycera convoluta-Nephthys hombergii* were found in association up to 43 m depth in medium and coarse clean sands located at the Ria outer zone with organic carbon values under 0.5 %. Seasonality was marked by *Spiochaetopterus costarum*, *D. glaucus* and *Chaetozone setosa* highest numbers all the surveing period long; fluctuations seemed to be linked to variations on sediment organic matter contents, grain-size and water temperature.

POPULATION DYNAMICS AND PRODUCTION OF *SCOLELEPIS GAUCHA* (POLYCHAETA, SPIONIDAE) ON THE SANDY BEACHES OF SOUTHERN BRAZIL. *Santos, P.J.P.* — (Université de Bordeaux I, Institut de Biologie Marine, 2 rue du Professeur Jolyet, 33120 Arcachon France). — Endemic in southern Brazil, Uruguai and Northern Argentina, *S. gaucha* (Orensanz & Gianuca, 1974) is the polychaete species with greatest intertidal abundance with densities up to 100,000 ind. $m^{-2}$. Four transects each with five stations were surveyed between 05/88 and 07/89. Sediment samples were sieved through 0.3 µm screens after preservation in 10 % formalin. After counting the animals, the width of the 5th setiger of 100 individuals, randomly chosen, was measured to determine the population structure. The program Compleat Elefan (version 1.10) was used to estimate growth parameters and mortality rate; production was estimated using both the Allen's method (Z = P/B) and Crisp's growth method 3A (production for stocks with recruitment, age classes not separable). *S. gaucha* presented a multiannual life cycle (with two cohorts each year) which was related to the diffusion pattern necessary to maintain its endemic distribution on a coast with strong seasonal processes. The large numerical variation observed between the two cohorts was interpreted as a result of densodependent mechanisms. The spatial differences observed for mortality rates (Z varying from 3.25 to 11.40) were associated to variations of the intertidal stability as expressed by the different sedimentological zones which were found between transects. Although differences in growth were observed between the cohorts, a general von Bertalanffy model modified for seasonal growth was proposed: $L(t) = 0.88\{1-\exp[2.655\ (t + 0.036) - (0.127)\sin(2\pi\ (t-0.05))]\}$. These differences were caused by the temporal modification of beach profile which benefited the first cohort food uptake. The high values of mean annual biomass (between 2 and 35 $g.m^{-1}$ AFDW) and production (between 6 and 114 $g.\ m^{-1}.\ yr^{-1}$ AFDW for Allen's method) reveal the importance of this species as one of the principal components of the midlittoral community.

AN ULTRASTRUCTURAL STUDY OF NEPHRIDIAL SYSTEM IN TWO NERILLIDS: *NERILLA JOUINAE* AND *TROCHONERILLA MOBILIS* (POLYCHAETA). *Saphonov, M.V. & Tzetlin, A.B.* — (Department of Invertebrate Zoology, Moscow State University, Moscow, 119899, Russia). — Fine structure of nephridia of representatives of two nerillids genera *Nerilla jouinae* and *Trochonerilla mobilis* were studied with the help of TEM technics. Nephridia of nerillids are paired segmental organs, they are absent in genital segments. Protonephridia of Trochonerilla mobilis consist of terminal cell, channel part and pore cell. Terminal cell forms a weir formed by approximately 40 rods and has 9-12 long cilia. Nucleus of this cell situated terminally. Lumen of nephridial duct belongs to extracellular type. There are microvilli and cilia in the duct's lumen. The endocytotic activity on the membrane of channel cells was found. Aberrant nephridia without terminal component (funnel or weir-system) were observed in one of fertile males of *T. mobilis*. *N. jouinae* has metanephridia, typical for this genus. Ducts has a loop and this part of nephridia forms a compact cell-mass, surrounded by squamous coelomic epithelium. In the area of the loop ducts lumen is intracellular. Cilia and microvilli also represented in the channel lumen. Nephridia of studied nerillids have the different levels of organization. On the one hand, correlation between metanephridia and presence of well developed blood system in *N. jouinae* and between protonephridia and absence of blood system in *Trochonerilla* on the other hand agree with Ruppert & Smith view on the diversity of nephridia.

THE EFFECTS OF RATE OF FOOD SUPPLY, INTRA-SPECIFIC DENSITY, INTERINDIVIDUAL RELATIONSHIPS AND ENVIRONMENTAL STRESS ON THE GROWTH OF JUVENILE *HEDISTE (NEREIS) DIVERSICOLOR* (ANNELIDA: POLYCHAETA) UNDER LABORATORY CONDITIONS. *Scaps, P., Retière, C., Desrosiers, G. & Miron, G.* — (Laboratoire Maritime, 17, avenue George V, B.P. 28, 35801 Dinard, France). — In a series of controlled experiments designed to determine the factors wich regulate the growth of juvenile *Hediste (Nereis) diversicolor* (O.F. Müller), tetramin was used as food, under conditions of constant temperature (19 ± 1°C) and salinity (38 P.S.U. ± 3). A ratio of 3.33 mg tetramin. $ind^{-1}.\ day^{-1}$ maintains an optimal growth rate but does not increase the rate of survival. When intra-specific density is above 3,000 ind. $m^{-2}$, the effect is manifested in a decrease in both weight per individual and rate of survival. Due to the effects of mortality (50 to 60 %), the densities of individuals obtained at the end of the experiment were similar to those observed in our sampling site in spring (about 2,000 ind. $m^{-2}$). Following a period of 50 days of rearing under controlled

Source : MNHN, Paris

conditions, individuals attained the same weight as adults collected *in situ*. A certain number were sexually differentiated (36-64 %) or mature (0-17 %). According to published data, adults do not mature until they are between 12 or 36 months old (depending on geographical location). Laboratory rearing of several month old juveniles did not lead to an increase in density (compared to that in nature) despite the absence of predators. Instead, the high frequency of handling of the worms (including changes of temperature), produces similar negative results. A variability is obtained between weights of individuals reared either in isolation or in groups, depending on whether the juveniles are collected in winter or spring. The weight of juveniles collected in spring is reduced when reared in isolation; but that of juveniles collected in winter is not affected in either conditions.

PROTEINS AS TAXONOMIC MARKERS IN THE POLYCHAETE TAXON *NEPHTYS*. *SCHMIDT, H. & WESTHEIDE, W.* — (Spezielle Zoologie, Fachbereich Biologie/Chemie, Universität Osnabrück, Postfach 4469, D-4500 Osnabrück, Germany). — Species of the genera *Nephtys* and *Aglaophamus* from intertidal and subtidal sediments of the Baltic, the Kattegatt, the southern North Sea and the western Channel area were investigated for (1) six isozymes and (2) for unspecific protein patterns. The separation of proteins was performed in polyacrylamid gels by isoelectric focusing (IEF). All of the nephtyid species which RAINER recently listed for this region could be discriminated by these two biochemical methods. There is evidence, however, that *Nephtys longosetosa is* a complex of two morphologically identical species. Suitability of protein data obtained by IEF is especially high for the separation and identification of single juvenile nephtyid specimens which usually are difficult to distinguish on conventional morphological features. Surprisingly the investigations showed lack of any genetic polymorphism within populations and between geographically separated populations of *Nephtys caeca, N. cirrosa* and *N. hombergii*.

REPLACEMENT OF CHAETAE IN ATOKOUS *NEREIS GRUBEI* (ANNELIDA, POLYCHAETA, NEREIDIDAE). *SCHROEDER, P.C.* — (Dept. of Zoology, Washington State University, Pullman, WA 99164, USA). — In addition to the well-known replacement of atokous chaetae with paddle chaetae during reproductive metamorphosis (SCHROEDER, 1967) nereid polychaetes regularly replace old atokous chaetae with new ones. Autoradiograms of sections of gameteless and young female individuals injected with tritiated thymidine reveal not only that chaetal replacement takes places periodically in regular cohorts, but that developing atokous chaetae incorporate the radiaoactive precursor into their matrix, providing an indicator for the rate of matrix deposition. The acicula of some individuals also incorporate H3-TdR into the basal portion of their matrix. The cycle of setal replacement will be described, and the utility of this information for future studies of the cellular mechanisms of chaetogenesis will be discussed.

GENOME SIZES AND CONSTITUTIVE HETEROCHROMATIN IN SPECIES OF *OPHRYOTROCHA* (POLYCHAETA). *SELLA, G., REDI, C. A., RAMELLA, L. & SOLDI, R.* — (Department of Animal Biology, University of Turin, Italy). — Genome size is a widely used parameter in studies on the evolution of various groups of organisms. We examined the heterochromatic and 2C nuclear DNA content of the ten best known species of the Polychaete genus *Ophryotrocha*, by means of C-banding technique and microdensitometric determination of Feulgen dye content of interphasic nuclei. Mesopsammic polychaete of the genus *Ophryotrocha* are very small, progenetic and morphologically very similar worms. They have been widely used in studies on problems of general evolutionary biology. Diploid chromosome numbers are either 6, 8, or 10, according to the species. Chromosomes are all metacentric or submetacentric and no interspecific significant differences were observed in karyotypic lengths. As for genome sizes, 8 out of 10 species showed a mean basic value of 0.4 pg. This value is among the lowest of the genome sizes of invertebrates so far investigated. A group of four gonochoric and morphologically indistinguishable species with 2n = 6 appears to be heterogeneous with regard to DNA content since one species (*O. . macrovifera)* has a genome size which is twice the basic value of the genus. Among the hermaphroditic species, one (*O. hartmanni*) has a mean genome size which is the triple the basic value. These interspecific differences in genome size appear to be paralleled by interspecific differences in constitutive heterochromatin content and could thus be due to saltatory replication of repetitive DNA. Moreover, in all species polyploid somatic nuclei were observed. Hypotheses about selective pressures that maintain such low amounts of nuclear DNA in this taxon are discussed.

THE POLYCHAETE ASSEMBLAGES INHABITING DIFFERENT TYPES OF BOTTOM SEDIMENTS IN ADMIRALTY BAY (ANTARCTICA). *SICINSKI, J.* — (University of Lodz, Department of Invertebrate Zoology and Hydrobiology, Laboratory of Polar Biology, 12/16 Banacha str., 90-237 Lodz, Poland). — The variety of habitats of different sediments in the nearshore zone of Admiralty Bay (King George Island, South Shetland Islands) is clearly reflected in the diversity of bottom fauna assemblages. The nature of sediments is highly dependent on the phenomena occuring on land near the shore. The neighbourhood of glaciers and the suspended particulate matter inflow through the subglacial streams seem to be the most important factors influencing the nature of sediments and in consequence the character of bottom assemblages. The distribution of 52 polychaete species in chosen regions of Admiralty Bay in the depth range between 4 and 150 m, evidently related to the kind of sediments, was studied, applying multivariate classification analysis *Leitoscoloplos kerguelensis* and *Ophelina syringopyge* were eurytopic and dominant species, reaching in the almost whole investigated area a high values of abundance, except of the shallowest parts of sandy bottom. In the parts of the bottom neighbouring the glaciers fast sedimentation of suspended matter occurs, forming a thick layer of clayey-silty

Source : MNHN, Paris

sedinents. The polychaete assemblage occuring here is characterized by low values of species richness and species diversity. *Ophelina cylindricaudata, Aricidea (Aedicira) antarctica* and *Tharyx cincinnatus* were here the dominant species. The polychaete fauna of nearshore areas situated far from glaciers was clearly different. In the sandy bottom of shallow sublittoral neighbouring the stony and sandy beaches to the depth down to about 30-40 m, the peculiar assemblage with *Scoloplos (Leodamas) marginatus, Capitella capitata, Rhodine* sp., *Cirrophorus brevicirratus* and *Travisia kerguelensis* as dominant species can be distinguished. In this area at greater depths sandy and silty-sandy botton prevails, settled by an extremely rich, diversified and most abundant assemblage. *Truberia gracilis* and *Aricidea (Acesta) strelzovi* were here very abundant, representing a group of dominant species. At greatest depths studied (100-150 m), also in the areas situated far from glaciers, silty sediments occur. Polychaete assemblage, resembling in general the last described one, was characterized here by the specific group of co-occurring species namely *Ephesiella* sp., *Artacama proboscidea, Streblosoma* sp., *Thelepus cincinnatus* and *Perkinsiana antarctica.* Apart from the assemblages detecting the gradual changes of polychaete fauna distributional patterns, corellated with increasing median particle diameter (very fine silt-fine silt-coarse silt-very fine sand), have been also observed.

WHAT *ARE PRIONOSPIO STEENSTRUPI, P. FALLAX* AND *P. DUBIA? SIGVALDADOTTIR, E. & MACKIE, A.S.Y.* — (Department of Zoology, Stockholm University, S-106 91 Stockholm). — MALMGREN (1867) erected the genus *Prionospio* to accomodate *P. steenstrupi,* a new spionid polychaete from northern Iceland. Characterized by four pairs of branchiae from setiger 2 (first and fourth pairs with pinnules, other pairs apinnate), the precise identity of this, the type species of the genus, has proven elusive. Consequently the taxonomy of the *P. steenstrupi*-complex has been subject to considerable confusion and instability. In the present study the three species of the complex occurring in the Northeast Atlantic (*P. steenstrupi, P. fallax* Soderstrom, 1920 and *P. dubia* Maciolek, 1985) are re-defined following examination of type and other available material. All are morphologically distinct species and have different geographical distributions. *P. steenstrupi* can be recognized by having first and fourth pairs of branchiae of equal length and with dense pinnules laterally, by having low dorsal crests on setiger 6 and on subsequent setigers, and by having neuropodial hooks from setigers 15-17. Further, it appears more northerly distributed than the two other species. *P. fallax* can be recognized by having first and fourth pairs of branchiae of equal length and with sparse pinnules laterally, by having high dorsal crest on setiger 7 and by having neuropodial hooks from setigers 12-13. The distribution is more southerly than for *P. steenstrupi;* from the North Sea to the Mediterranean. *P. dubia* can be recognized by having branchiae four much shorter than branchiae one and with dense posterior pinnules on both, by an absence of dorsal crests, and by having neuropodial hooks from setigers 18-21. The type locality for *P. dubia* is South Africa and the distribution for this species therefore seems very wide; from the North Sea to South Africa.

CHECKLIST AND BIBLIOGRAPHY OF POLYCHAETES FROM GREECE WITH SOME RECENT ADDITIONS. *SIMBOURA, N. & NICOLAIDOU, A.* — (National Centre for marine Research Aghios Kosmas, 16604 Hellinikon, Athens, Greece). — A checklist and bibliography of polychaetes from Greece, which lists 570 species of benthic polychaetes belonging to 46 families. For each species a list of the geographical localities where this has been recorded along with the respective bibliographical citations is provided. Some new findings for the polychaete fauna of Greece are reported. These are: *Auchenoplax crinita* Ehlers, 1887; *Galathowenia oculata* (Zaks, 1922); *Hesiospina similis* (Hessle, 1925); *Hydroides dianthus* (Verril, 1873); *H. nigra* (Zibrowius, 1971); *Lumbrinerides amoureuxi* Miura, 1980; *Opisthodonta pterochaeta* Southern, 1914; *Polycirrus plumosus* (Wollebaeck, 1912); *Sphaerosyllis brevicirrata* Hartmann-Schroeder, 1960; *Syllis torquata* (Marion & Bobretsky, 1875). A list of the references used as a source is supplied.

REPRODUCTIVE BIOLOGY AND LIFE CYCLE OF *BRANCHIOMMA LUCTUOSUM* (GRUBE, 1869) (POLYCHAETA, SABELLIDAE) IN THE MEDITERRANEAN SEA. *SORDINO, P. & GAMBI, M.C.* — (Laboratorio di Ecologia del Benthos, Stazione Zoologica "Anton Dohrn", Napoli, Italy). — Data on the reproductive traits and the life cycle of Polychaetes are still scarce with respect to the diversification of these organisms and to the implications that these aspects have for their ecology and phylogeny. In this optics we studied the reproductive biology of *Branchiomma luctuosum* (Grube, 1869), a rare Sabellid recently reported for the Mediterranean Sea. The population of *B. luctuosum* studied was found in a shallow *Cymodocea nodosa* meadow and in the surrounding hard substrates of the Island of Ischia (Gulf of Naples, Italy). From July 1990 to July 1991, at least 10 specimens of *Branchiomma* of different size classes were collected monthly, measured and fixed for the histological and ultrastrutural analysis of the gametogenesis. *B. luctuosum* proved to be a simultaneous hermaphrodite, because mature sperms and developing ovocytes were present in the coelom from July. Ripe eggs were observed in late September and October and gamet spawning occurred in October-November; in December all specimens were in a "spent" stage. From January germ cells occurred on the coelomic walls indicating the starting of a new gametogenic cycle. No discrete gonads were observed suggesting intra coelomic gametogenesis, a finding supported by the ultrastructural features of the immature ovocytes. The mature sperm has a typical "ect-aquasperm" structure that is considered a primitive character and is consistent with the free-spawning habit. Yet to be confirmed is the occurrence of self-fertilization. No egg protection, such as cocoons or tube incubation, was observed in the field, suggesting the existence of a pelagic larva, also supported by the size of the mature eggs. In the light of these data *B. luctuosum* seems to be a perennial iteroparous species with a discrete synchronic spawning event. This is the first reported case of such a mosaic of life cycle traits in Sabellid Polychaetes.

Source : MNHN, Paris

ECOPHYSIOLOGY OF THE SANDY BEACH INTERSTITIAL POLYCHAETE *POLYGORDIUS ESCHATURUS* (POLYGORDIIDAE): TOLERANCE AND PREFERENCE EXPERIMENTS. *Sousa-Santos, L. P.& Silva, V.M.A. da.* — (Departemento de Zoologia, Universidade de Rio de Janeiro, RJ-Brazil). — Laboratory experiments on tolerance and preference were designed to elucidate the importance of some ambiental factors on the ecology of *Polygordius eschaturus*, and to help the understanding of the distribution pattern of this interstitial species on a sandy beach in southeastern Brazil. The first results indicated that this species could be easily maintained for some weeks in mini-aquariums provided with sand and daily renovated sea water. The tolerance results were expressed by an index that considers both behaviour and survival of the animals, and were analysed by non-parametric statistics. *P. eschaturus* showed a great salinity tolerance since the animals survived in salinities between 10 and 50 P.S.U. and their behaviour was not affected between 20 and 40 P.S.U. These limits were the same for both gradual and abrupt salinity changes. For the temperature tolerance it was found that at 10 °C the animal behaviour was affected, at 20 °C and 30 °C the animals were not affected by temperature and at 40 °C all the animals died. At the salinities and temperatures tested, little interaction between these factors was observed. *P. eschaturus* showed photonegative and geopositive behaviour, nevertheless, migration toward the highest oxygen tension layer may overlay this last behaviour. This species has no attraction for single sediment grades, and may even die if maintained in those sediments. The animals showed a preference for natural sediment in contrast to sediment without organic matter. This species occurs at the midlittoral level of a coarse-sand beach where the salinity and temperature changes may be great, but the animals are present mainly between 10 and 20 cm in the sediment, probably to not be exposed to the greatest surface changes. Since the animals were attracted to the highest oxygen tension, at that depth the oxygen tension should be high, probably due to a good percolation of water through the coarse sediment. The specificity of this species to its natural sediment was probably related to the sediment selection and porosity and may explain its horizontal distribution on the beach. However, more experiments are necessary to confirm this hypothesis.

PRELIMINARY REPORT OF POLYCHAETE ASSEMBLAGES IN THE SOFT BOTTOMS OF THE CHAFARINAS ISLANDS (SOUTHWESTERN MEDITERRANEAN). *Torres-Gavila, F.J., Capaccioni-Azzati, R., Tena, J. & Garcia-Carrascosa, A.M.* — (Invertebrate and Marine Biology Laboratory, Department of Animal Biology, Faculty of Biological Sciences, University of Valencia, Burjassot E-46100, Valencia, Spain). — The Chafarinas Archipelago is located in the southern basin of the Alboran Sea, two miles from the Moroccan coast, near the Ouëd-Moulouya river mouth. This archipelago is composed of three volcanic rocky islets: Congreso, Isabel II and Rey Francisco. These islets are located on a horizontal shallow shelf. The shelf is about 15 m deep on its Southern side, but reaches depths of about 30-35 m on the Northern side. The bottoms around the islets are subject to an important discharge of fine sediments from the Ouëd-Moulouya river mouth. This supply of sediments determines to a great extent the settlement of different marine communities and particularly the polychaete fauna in this area. Here we present results of a study of the annelid polychaete assemblages on soft bottoms of the sedimentary shelf at 40 sampling stations distributed among the different sediment types found around the islets. We conducted a comparative analysis of the polychaete fauna in three major types of sediment (coarse muddy, fine sandy and gravel and coarse sandy bio-detritic bottoms) distinguished on the basis of their granulometric characteristics. Other environmental factors affecting the distribution of species are also discussed.

ON THE BIOLOGY AND ECOLOGY OF *SACCOCIRRUS PARVUS* GERLACH, 1953 (POLYCHAETA, SACCOCIRRIDAE). *Villora-Moreno, S.* — (Invertebrate and Marine Biology Laboratory, Department of Animal Biology, University of Valencia, Burjassot E-46100, Valencia, Spain). — *Saccocirrus parvus* is an interstitial polychaete inhabiting the midlittoral zone of the Mediterranean sandy beaches. This species is included in the *"papillocercus*-group" because the absence of pharyngeal bulb, presence of genital organs on both sides of the segments, and lack of ventral ciliary patches or tracks. Despite the cosmopolitan condition attributed to *"papillocercus*-group", *S. parvus* is known only from the Mediterranean Sea, and information on this species after its original description (Gerlach, 1953) is scarce. In this paper, a redescription of the species is provided through vital and *post mortem* coloration techniques for optical microscopy and SEM observations. Details of the male and female reproductive systems, morphology of epidermic metameric glands, and adhesive glands, morphology of the three types of setae and other features from SEM micrographs, are given for the species. These last characters are helpful for species differentiation in the *"papillocercus*-group". A quantitative study on spatial distribution of *S. parvus* was achieved using a standard corer. The different zones of the beach were sampled. Abundance of *S. parvus* increased in the turbulent zones, reaching a maximum in the *Otoplana*biocenosis level, with densities of 660 ind. $ml^{-1}$. A long-time survey of three years allowed us to determine the fertile period of the species. Mature individuals were observed during the temperate months, from April to September. The size of the specimens as well as the morphology of the pygidium seems to be correlated with the sediment granulometry. A discussion of these observations is reported through a morphometric study. Finally, some results of feeding are in agreement with figures found by authors for other co-generic species. The carnivorous preferences of this species is deduced from the observation of Harpacticoids and Nematodes in the gut contents of living specimens.

THE ELECTRONIC *PALOLA* OR COMPUTER PUBLICATION OF SYSTEMATIC PAPERS. *Ward, L.A. & Fauchald, K.* — (National Museum of Natural History, Smithsonian Institution, NHB Stop 163 Washington D.C., U.S.A.). — Very few journals will accept large systematic studies. They are expensive to print and the audience is limited. Recent computer

Source : MNHN, Paris

software makes electronic publishing an attractive alternative. Within a fixed, electronic "journal" format, an author can create a publication with keys, text, illustrations and cited literature. An electronic "journal" may be issued four times a year as a compact disc, or perhaps only once a year. Under any circumstances, if the editor of a journal receives a computer file in good condition from the author, the cost of such a journal would be about 1/4 of current printing costs for the same amount of material. Reviewing papers for such publication is as easily arranged as that of paper publications. The security of a computerized paper does not differ in kind from that of a normal journal: copiers and optical character readers makes it possible for any interested person to copy and computerize, as a database or a word-processing document any paper in print. It may be slightly easier to download a portion of a computerized publication, but that difference is trivial. As an example, we have transferred into computer format a recently completed (and submitted) paper describing types of *Palola*. We will demonstrate advantages and drawbacks in this new technology and will also discuss the ramifications of this kind of development for production of journals by non-profit corporations, such as various societies and by profit-making ventures such as the various publishing houses.

STUDY OF THE BIOGEOCHEMICAL GRADIENTS SURROUNDING POLYCHAETE TUBES IN SEDIMENTS OF THE LAURENTIAN TROUGH. *WHITE, C., JUNIPER, S.K. & DESROSIERS, G.* — (Centre Océanographique de Rimouski, 310, Allée des Ursulines, Rimouski, Québec, G5L 3A1, Canada). — This study compares biogeochemical gradients generated by tube construction and irrigation by two species of polychaete (*Maldane sarsi* and *Ampharete acutifrons*) in deep-water sediments (350 m) of the Laurentian Trough. While both species are detritivores, *M. sarsi* lives and feeds in a head-down position in its tube. Trace metal and organic matter content, granulometric properties and bacterial abundance were analysed in tubes and surrounding sediments for each species. Gramulometric analysis show that both species sort sediments while building their tubes. Bacterial counts, organic matter and trace metals were most concentrated in sediments of the inner tube wall of both species. Vertical gradients are also evident and appear to reflect different feeding habits and depths at which each species occurs in its tube. Using abundance data for both species we extrapolate to assess the overall impact of tube construction and occupation on sediment biogeochemical processes in the Laurentian Trough.

IMMUNOHISTOCHEMICAL OBSERVATIONS ON THE NERVOUS SYSTEMS OF TWO *DINOPHILUS* SPECIES DEMONSTRATE DIFFERENCES IN NEURONAL ARRANGEMENT AND NEUROCHEMICAL EQUIPMENT. *WINDOFFER, R. & WESTHEIDE, W.* — (University Osnabrück, Fb Biology Chemistry, Barbarastr. 11, D-W-4500 Osnabrück, Germany). — Investigations of the nervous system of *Dinophilus gyrociliatus* and *D. taeniatus* with immunohistochemical methods lead to information on the nervous anatomy and the chemical nature of their neuroactive substances. The results gave new insights into special characteristics of these aberrant polychaetes, their proposed progenetic origin, the extreme dimorphism of *D. gyrociliatus* and the obligate encystment within the life cycle of *D. taeniatus*. Antibodies against the amines octopamine and serotonin, and the peptides FMRFamide, CCK and $SCP_B$ stained various subsets of perikarya and fibers. Antibodies against several other peptides showed no positive reactions leading to the assumption of a reduced neurochemical equipment in *Dinophilus* compared to other polychaetes. This is in accordance with a proposed highly derived nature of the Dinophilidae.There is a general correspondence in the staining pattern of the females of *D. gyrociliatus* and *D. taeniatus* with most antibodies. Nevertheless, important differences can be shown in details, e.g. in the neuronal arrangement and neurochemical equipment of the stomatogastric nervous system and the nerves of the body wall. These variations can be explained by different feeding behaviour and ciliation of the body wall. Further dissimilarities cannot be explained in this way. Octopamine-like immunoreactivity can only be found in *D. taeniatus*. Anti-Serotonin and anti-FMRFamide stained a wide range of nervous elements in both species with clear differences in number and position of positive neurons. Even immunogold stainings show different populations of neurovesicles in both species. These results are surprising because of the assumption that serotonin, FMRFamide and octopamine should be involved in fundamental neuronal activities such as movement and central neuronal integration which should be more or less identical in both species. These differences might be related to a rearrangement of the *D. taeniatus* nervous system that enables encystment.

PRELIMINARY REPORT ON VEGETATIVE REPRODUCTION OF *MALDANE SARSI* ARDWIDSSON, 1911 (POLYCHAETA, MALDANIDAE) OFF ELEPHANT ISLAND, ANTARCTICA. *WRZESINSKI, O.J.* — (Univers. Martin Luther King Platz 3, 2000 Hamburg 13). — A rare case of a wide-scale vegetative reproduction of *Maldane sarsi* is described. The material was collected during the V International Antarctic Expedition on board of the r/v "Polarstern", cruise 9 (1986), northwards of Elephant Island on the depth of 227 m. Respective stages of that phenomenom are presented.

CONTRIBUTION TO KNOWLEDGE OF OFFSHORE POLYCHAETE FAUNA IN THE NORTHERN ADRIATIC. *ZAHTILA, E.* — (Center for Marine Research, "Ruder Boskovic" Institute, 52210 Rovinj, Croatia). — At three coenobioses located in the North Adriatic offshore area, qualitative and quantitative structures of the Polychaete fauna have been studied, within the period 1982 to 1987. A total of 101 species were noted. The faunal composition, and species distribution, with regards to sediment characteristics and trophic relations were discussed.

Source : MNHN, Paris

Ont collaboré à la réalisation de cet ouvrage :

Saisie des textes et mise en page :
G. BELLAN, M. BHAUD, J.-C. DAUVIN, J.-C. DUCHÊNE, P. GILLET, L. LAUBIER et C. RETIÈRE

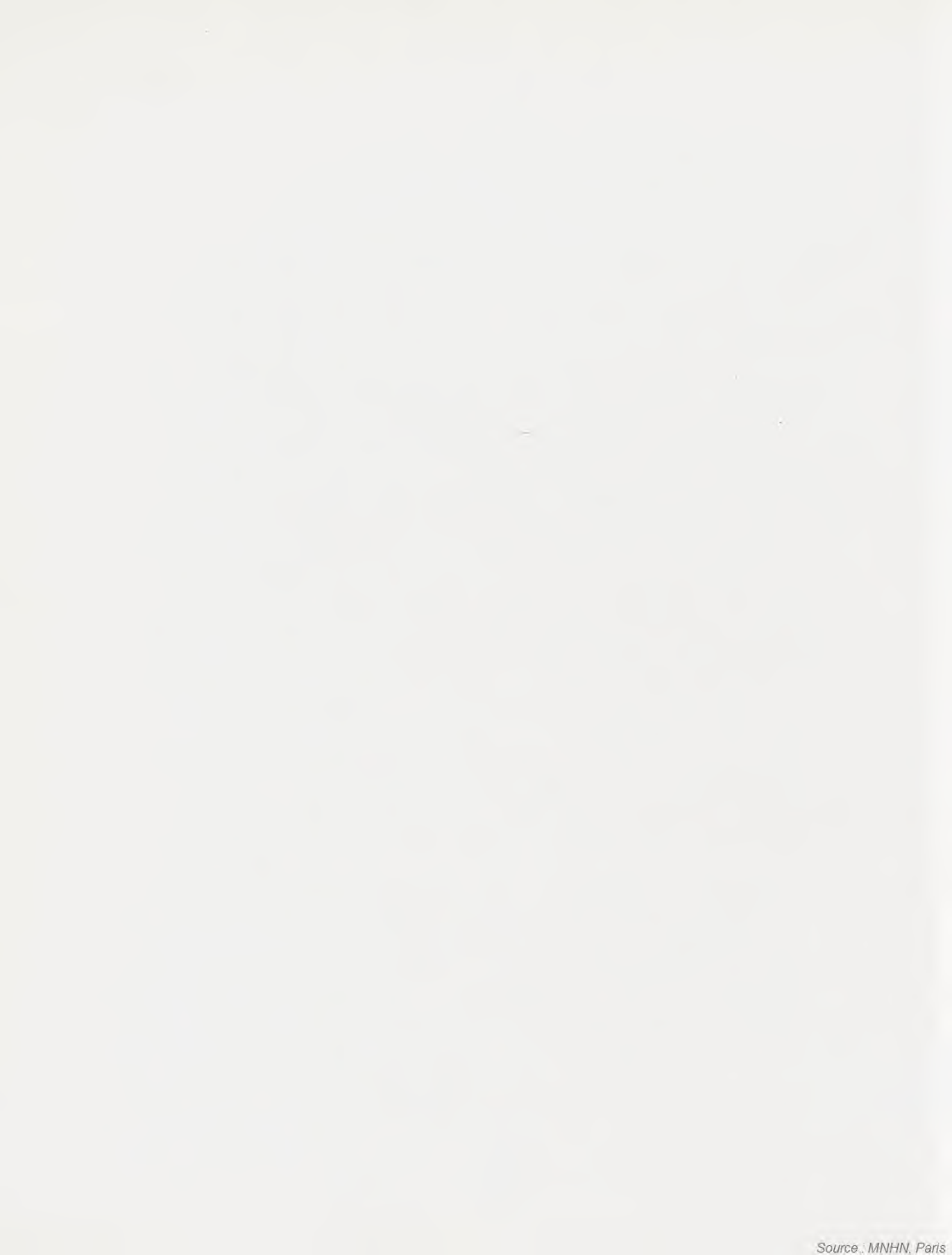
Vérification des manuscrits et des épreuves :
J.-C. DAUVIN, D. REISH et J. VOVELLE

La mise en forme du manuscrit final a été réalisée par L. LAUBIER
sur MacIntosh IIci avec logiciel WORD 5.1

*Impression :* F. PAILLART - ABBEVILLE
*Date de distribution : 20 décembre 1994*
*Dépôt légal : Décembre 1994*
*N° d'impression : 9186*

BIBL.
MUSÉ
PARIS

Source : MNHN, Paris



Source : MNHN, Paris

# DERNIERS TITRES PARUS

## *RECENTLY PUBLISHED MEMOIRS*

A partir de 1993 (Tome 155), les *Mémoires du Muséum* sont publiés sans indication de série.
*From 1993 (Volume 155), the* Mémoires du Muséum *are published without serial titles.*

Tome 161 : Alain CROSNIER (ed.), 1994 — Résultats des Campagnes MUSORSTOM. Volume 12. 610 pp. (ISBN 2-85653-212-8) 600 FF.

Tome 160 : Nicole BOURY-ESNAULT, Maurizio PANSINI, & Maria Jesus URIZ, 1994 — Spongiaires bathyaux de la mer d'Alboran et du Golfe ibéro-marocain. 174 pp. (ISBN 2-85653-213-6) 300 FF.

Tome 159 : Pierre ROBBE, 1994 — Les Inuit d'Ammassalik, Chasseurs de l'Arctique. 389 pp. (ISBN 2-85653-270-1) 360 FF.

Tome 158 : Alain CROSNIER (ed.), 1993 — Résultats des Campagnes MUSORSTOM. Volume 11. 426 pp. (ISBN 2-85633-208-X) 500 FF.

Tome 157 : Loïc MATILE, Judith NAJT & Simon TILLIER (eds), 1993 — Zoologia Neocaledonica. Volume 3. 218 pp. (ISBN 2-8563-205-5) 280 FF.

SÉRIE B (BOTANIQUE) :

Tome 32 : Claudine FRIEDBERG, 1990 — Le savoir botanique des Bunaq. Percevoir et classer dans le Haut Lamaknen (Timor, Indonésie). 304 pp. (ISBN 2-85653-177-6) 350 FF.

Tome 31 : Odile PONCY, 1985 — Le genre *Inga* (Légumineuses, Mimosoideae) en Guyane française. Systématique, Morphologie des formes juvéniles, Écologie. 124 pp. (ISBN 2-85653-135-0) 210 FF.

Tome 30 : Lucile ALLORGE, 1985 — Monographie des Apocynacées — Tabernaemontanoïdées américaines. 216 pp. (ISBN 2-85653-132-6) 280 FF.

Tome 29 : Monique KEDDAM-MALPLANCHE, 1985 — Le Pollen et les stomates des Gardéniées (Rubiacées) du Gabon. Morphologie et tendances évolutives. 109 pp. (ISBN 2-85653-131-C-8) 220 FF.

Tome 28 : Marie-France ROQUEBERT, 1981 — Analyse des phénomènes pariétaux au cours de la conidiogenèse chez quelques champignons microscopiques. 79 pp. (ISBN 2-85653-116-4) 130 FF.

SÉRIE C (SCIENCES DE LA TERRE) :

Tome 56 : Jean-Paul SAINT MARTIN, 1990 — Les formations récifales coralliennes du Miocène supérieur d'Algérie et du Maroc. 373 pp. (ISBN 2-85653-170-9) 392 FF.

Tome 55 : Georges BUSSON (ed.), 1988 — Évaporites et hydrocarbures. 144 pp. (ISBN 2-85653-155-5) 180 FF.

Tome 54 : Monette VÉRAN, 1988 — Les éléments accessoires de l'arc hyoïdien des poissons téléostomes (Acanthodiens et Osteichthyens) fossiles et actuels. 114 pp. (ISBN 2-85653-154-7) 150 FF.

Tome 53 : Donald E. RUSSELL, Jean-Pierre SANTORO and Denise SIGOGNEAU-RUSSELL, 1988 — Teeth Revisited : Proceedings of the VIIth International Symposium on Dental Morphology. 462 pp. (ISBN 2-85653-148-2) 625 FF.

Tome 10 : Jacques ROGER, 1962 (Réimpression/Reprint 1988) — BUFFON. Les Époques de la nature. Édition critique. 344 pp. (ISBN 2-85653-160-1) 100 FF.

Prix hors taxe, valides jusqu'à décembre 1995. Frais de port en sus. Vente en France : TVA 2,10 %.

*Prices in French Francs are valid until December 1995. Postage not included.*

Source : MNHN, Paris

Every three years, since 1983, an International Polychaete Conference has been organized to provide a forum for the communication of our knowledge of this group. The proceedings of these Polychaete Conferences have remained important reference books for the study of Polychaetes, in the absence of a scientific journal specialized on these organisms. This volume of " Mémoires du Muséum national d'Histoire naturelle " publishes all the communications presented at the fourth International Conference held in Angers in 1992, with a total of sixty five papers selected on the basis of a peer review process following the Conference, and 101 abstracts. The papers are classified into five topics as a large amount of studies on polychaete demonstrate the various approaches in this group : Cytophysiology, development and reproduction (seven papers), Genetics and morphology (eight papers), Phylogeny and taxonomy (19 papers), Ecology and biogeography (29 papers) and Culture and valorisation (two papers). Up to date reviews of several subjects are included, with a significant number of new data. The phylogenetic positions of some families are discussed as a basis for new hypotheses on the relationships between Polychaete families. Three genera and 10 species new to science are described in this volume. The future of polychaetes exploitation should be their culture and valorisation.

Jean-Claude DAUVIN, Dr ès Sciences, spent thirteen years as a researcher with the Centre National de la Recherche Scientifique at the Biological Station of Roscoff, Brittany, and is now Professor at the Muséum national d'Histoire naturelle, Curator of worms. He is particularly interested in benthic communities and Polychaete populations from the English Channel, and focuses on the systematics and the phylogeny of Opheliidae.

Lucien LAUBIER, Dr ès Sciences, Director at the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Professor at the Institut Océanographique de Paris, is Counsellor for Science and Technology in the Permanent Representation of France to the European Union in Brussels. He has studied Polychaetes for some 35 years and is still active in systematics, phylogeny and biogeography of Polychaetes, in particular Alvinellids from deep-sea hydrothermal vents and Mediterranean Polychaetes.

Donald J. REISH, Ph. D., Emeritus Professor at California State University in Long Beach, is currently consultant with U.S. Bureau of Standard and U.S. Army Corps of Engineers. He has studied Polychaetes for more than 40 years and his classic work " An ecological study of pollution in Los Angeles Long Beach harbors " (1959) is considered to be the corner stone of modern benthic studies in polluted areas. He is currently involved in toxicological studies using Polychaetes as test organisms.

ÉDITIONS
DU MUSÉUM
57,
RUE CUVIER
75005 PARIS
ISBN 2-85653-214-4
ISSN 1243-4442

PRIX : 398 FF TTC (France)
390 FF HT (Étranger)

Source : MNHN, Paris

COM

MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE TOME 162 ZOOLOGIE

# ACTES DE LA 4ÈME CONFÉRENCE INTERNATIONALE DES POLYCHÈTES

Jean-Claude DAUVIN,
Lucien LAUBIER &
Donald J. REISH

R. 260 C1

Source: MNHN, Paris